MEASURING AUDITORY THRESHOLDS IN BRUSHTAIL POSSUMS (*TRICHOSURUS VULPECULA*)

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ABSTRACT

A total of 9 brushtail possums (*Trichosurus vulpecula*) were trained to perform a two-manipulanda, conditional discrimination task. The possums learned to press a right lever in the presence of a tone (80 dB(A)) during tone-on trials, and a left lever in the absence of the tone on tone-off trials. Overall sessions of 11 conditions contained tone frequency between 100 Hz and 35 kHz were tested. Each condition contained training and then probe sessions. In training sessions, the possums were presented with tone-on and tone-off trials, pseudo-randomly. Once the possums responded with over 90% accuracy for five consecutive sessions, then probe sessions were introduced. Probe sessions were similar to the training sessions, except that the tone intensity for tone-on trials was reduced by 8 dB(A) across blocks of 20 trials until their response accuracy in a block fall below 60% or reached 24 dB(A). Data were analysed using overall percentages correct and log *d* analysis. Both measures indicated that overall response accuracy decreased for all possum as tone intensity reduced. Based on these data analyses, threshold values were calculated using the criterions at 75% correct and a log *d* of 0.48. The threshold values for each possum and across all possums were plotted as a function of the tone frequency to produce an audiogram. A curvilinear regression was fitted for each threshold values. The functions of both measures were very similar. Both audiograms showed that the possums could hear the tones between 100 Hz and 35 kHz, and were most sensitive to tones between 15 and 20 kHz. This experiment involved many difficulties with producing and measuring tones especially outside of human hearing range. Due to these difficulties, several problems and concerns were raised during the experiment, these were discussed in this study and also recommendations for future research were then presented.

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Part A

Brushtail possums (*Trichosurus vulpecula*) are omnivores and are serious pests both to indigenous forests and to agriculture in New Zealand. The effects of possums browsing plants on forest ecosystems are well documented. These include changes in the composition of some plant communities (Atkinson et al., 1995; Cowan, 2001; Nugent et al., 2000; Payton, 2000). Possums are also predators that can seriously affect native invertebrate and bird populations in New Zealand (Innes et al., 1995; Meads et al., 1984; Powlesland et al., 2003; Sadleir, 2000; Veltman, 2000). In New Zealand, possums are spreading diseases, such as tuberculosis, to farm animals (Ministry of Agriculture and Forestry, 1994).

According to the Parliamentary Commissioner for the Environment in 1994 (p.8), The New Zealand Government funded more than 58 million dollars in controlling the possum population that included research on possums (Ministry of Agriculture and Forestry, 1994).

A variety of technologies are currently applied to control the possum population in New Zealand. For example, poisoning controls (i.e., spreading baits containing 1080, Brodifacoum, Cyanide or Cholecalciferol: Henderson, O'Connor & Morgan, 1999) and manual controls (i.e., shooting or trapping; Ministry of Agriculture and Forestry, 1994) have been employed. Despite the use of these techniques, a significant number of possums still survive (Henderson, O'Connor & Morgan, 1999).

Brockie, Fitzgerald, Green, Morris and Pearson (1984) suggested that to be able to control the possum population effectively using those current methods, more research is required, particularly, on possums' basic behaviour, their sensory perception and food preferences. Clout and Sarre (1997), and Wynne and

McLean (1999) also pointed out the lack of research studies especially in the area of learning and sensory abilities of brushtail possums, and suggested that more research is needed. Signal (2002) also noted that their auditory ability has been poorly researched and suggested the need for more research in this area.

Possum's Auditory Abilities

There are three main types of data, anatomical, physiological and behavioural information, used in investigating the auditory abilities of animals (Blough & Blough, 1977). There are a few publications for brushtail possums and/or other marsupials in each of these studies.

Anatomical Studies

Possums are marsupials and Aitkin, Bush and Gates (1978), and Aitkin, Gates and Kenyon (1979) reported that, although marsupials share many similarities in neocortical features with mammals, there are some clear anatomical differences. One major difference is that marsupials have a smaller corpus callosum than placental mammals, and only diprotodontid marsupials have developed a commissure that connects at the dorsal regions of the neocortex of the two hemispheres (Abbie, 1939; Heath & Jones, 1971; Johnson, 1977). Marsupials have a distinct arrangement of cortical neurons, in which, unlike placental mammals, the cell bodies of the deeper layer of the cortex are often thin and arranged in rows which run parallel to the cortical surface (Johnson, 1977). Aitkin, Gates and Kenyon (1979) suggested that it is possible that these structural differences could affect the functional arrangement of the auditory cortex in brushtail possums.

Gate and Aitkin (1982) investigated the auditory cortex of brushtail possums using a microelectrode mapping survey. They reported that brushtail

possums have an orderly representation of sound frequency in a “cochlear place” in the auditory cortex, which is similar to one found in some mammals such as macaque monkeys, owl monkeys, grey squirrels and cats. However, brushtail possums have a dorsal-to-ventral organization of high-to-low frequencies, while mammals normally have an anterior-posterior orientation. Another difference is that there is only one cochlear representation in the auditory cortex for brushtail possums, whereas mammals often have multiple auditory cortical fields. Usually mammals develop large areas of the auditory cortex related to specific frequencies, especially those needed for their survival. However, brushtail possums do not show such phenomena, and the reason for this is unclear.

Fernández and Schmidt (1963) investigated the structure of marsupial’ ears and found that the cochlear in both opossums (*Dedelphis Viriginiana*) and placental mammals (guinea pig, cat and monkey) is coiled, narrowing to an apex, and looks like a snail shell.

Physiological Studies

There have been some physiological studies on possums’ auditory systems. Gates and Aitkin (1982) conducted a microelectrode mapping survey on brushtail possums’ auditory cortex, and found their best frequency range to be between 330 Hz and 39 kHz with the greatest sensitivity of between 17 and 19 kHz (10dB SPL). This frequency range was quite different from mammals.

Aitkin, Gate and Kenyon (1979) investigated the differences between peripheral auditory characteristics in brushtail possums and cats. Cochlear micro-phonic potentials (CM) at the round window were used to measure the response to several sounds varying intensities and frequencies. They found that the threshold intensity required to elicit responses from nerves in the cochlear in possums ears

was 50 µV CM at frequencies between 0.4 and 10 kHz for cats and this was smaller than possums, and the possums' hearing is more sensitive between 0.1 and 0.4 kHz than cats.

Similar to the placental mammals, the frequencies that brushtail possums are most sensitive to were related to their calls (Aitkin, Gate & Kenyon, 1979). Winter (1976) recorded at least 24 calls of brushtail possums using a portable tape recorder that was manufactured specially for this purpose. He found that the frequencies of possums' calls were approximately between 0.5 kHz (chatter calls; a loud rough call that carries over distances of 100 to 200 m) and at least 12 kHz (click calls; a sharp sound which carries little more than 5 to 10 m). This was a similar frequency range to the one found from the physiological study.

Behavioural Studies

To the author's knowledge, there is only one published study investigating the auditory ability of brushtail possums, behaviourally. Signal, Foster and Temple (2001) tested the ability of six brushtail possums to discriminate a tone of one frequency (880 Hz) at a variety of decibel levels (dB (A)) from background noise. The possums were able to discriminate this tone well at 80 dB (A), although their discrimination ability deteriorated as the intensity of the tone was decreased. Signal et al. (2001) found that, on average, the possums detected sound accurately until approximately 36 dB (A) for this 880 Hz tone.

As this was the only frequency investigated this is not sufficient information to understand the extent of the auditory ability of brushtail possums.

Summary

As Blough and Blough (1977) pointed out, anatomical, physiological and behavioural data provide different types of information about audition. No single

method provides the best information, and it is important that all three types of data are obtained to understand possums' auditory abilities. With only one behavioural study showing that brushtail possums could detect a tone (at only one frequency), it is clear more data are needed. One aim of this present study was to use a behavioural method to gather more data on the frequencies at which the brushtail possums can discriminate a tone from background noise, and further what intensities are required for this.

Part B

Behavioural Methods

There are several kinds of behavioural methods that have been used for the investigation of the auditory abilities of animals. Blough and Blough (1977) pointed out that the commonly used behavioural methods involve operant conditioning. This entails training animals to make an arbitrary response in the presence and/or the absence of certain stimuli. Various operant techniques have been developed for assessing sensory abilities (e.g., conditioned suppression, go/no-go and yes-no procedures), and each method has advantages and disadvantages.

Conditioned Suppression

Conditioned suppression has widely been used method in psychophysics experiments (Blough & Blough, 1977). In this procedure, an animal is typically trained to perform in a particular way (e.g., licking a water spout) that is maintained by the delivery of reinforcer (e.g., water) until the rate of the behaviour is stable (Ravizza & Masterton, 1972). Once the rate is stable (or a stable-baseline was achieved), a warning stimulus (e.g., a tone) is presented for a

certain period of time, followed by the delivery of an aversive event (e.g., electric shock) to the animal. The intensity of the warning stimulus is changed and theoretically, when the animal can perceive the stimulus, while the stimulus is present, a lower rate of behaviour, compared to the stable baseline rate, would be observed (Blough & Blough, 1977; Ravizza & Masterton, 1972). For example, Ravizza, Heffner & Masterton (1969) assessed the auditory capacity of two wild-born opossums (*Didelphis virginianus*) using the conditioned suppression technique. These opossums were trained to lick a water spout using a variable ratio schedule of reinforcement. Once the rate of water licking behaviour was stable, a tone was played and an unavoidable electric shock was delivered to their feet. The tone was varied in its frequency but set at 80 dB (A). The opossums' licking behaviour suppressed when the tone was present and the opossums were deemed to have perceived the stimulus. The results showed that the opossums were sensitive to the frequencies between 0.5 to 60 k/s. A common disadvantage with this method is the difficulty in obtaining the stable baseline response rate (Blough & Blough, 1977).

One Manipulandum Methods

A single manipulandum method is often referred as a go/no-go method, in which a stimulus (discriminative stimulus or S^D) is the signal of the availability of a consequence for an animal (Blough & Blough, 1977). If the stimulus is present, the consequence will be available, and the animal would be more likely to respond on the manipulandum. When the stimulus is absent, the consequence will be absent, and thus theoretically the animal would be less likely to respond on the manipulandum (Blough & Blough, 1977).

Behaviour, responding on the manipulandum under the presence of S^D, can be maintained by positive or negative reinforcement. For example, when the behaviour is maintained by positive reinforcement, the consequence, termed a positive reinforcer that is something an animal highly prefers (e.g., food for a food deprived animal) will be delivered following the response. In such case, the animal responds on the manipulandum to gain access to the preferred item, and thus the behaviour is maintained by the positive reinforcement. When the behaviour is maintained by negative reinforcement, then the consequence, termed negative reinforcer, is the termination of an aversive event to the animal (e.g., electric shock). In this case, the animal responds on the manipulandum to terminate the delivery of the aversive consequence, under the presence of the S^D.

Blough and Blough (1977) suggested that one disadvantage with go/no-go methods is that an animal generally responds on the manipulandum regardless of the presence or absence of a S^D, consequently the number of responses the animal made when the signal is absent is generally high. Therefore it is hard to determine if the responses are made because the animal detected the signal or not. Moreover, the use of an aversive consequence might result in disrupting the animals' behaviour in some other ways (Blough & Blough, 1977).

Two Manipulanda Methods

Another operant technique requires two-response manipulanda. Unlike one manipulandum methods, two manipulanda methods require an animal to respond on one of the two manipulanda when a stimulus is present, on the other when the stimulus is absent. Therefore this can minimise the risk of the animal excessively responding on one manipulandum regardless of signal presentations (Green & Swets, 1966).

One method using two-response manipulanda is called a yes-no procedure. This procedure uses two-response manipulanda (i.e., a left and right lever), and this typically has two types of trials, called stimulus-on and stimulus-off trials. In the stimulus-on (or on) trials, also termed signal + noise (s + n) trials, an animal is typically presented with a stimulus (Green & Swets, 1966). In the stimulus-off (or off) trials, also called noise only (n) trials, there is no stimulus presented, and thus the animal is exposed to the background noise only (Green & Swets, 1966). The animal's correct response (responding on one manipulandum in the on trials and on another manipulandum in the off trials) is reinforced by giving access to a reinforcer (e.g., often preferred food). If the animal responds incorrectly, the animal typically experiences a blackout (light is turned off and experimental chamber is stopped operating) for a certain period of time and no reinforcer is given. There is usually an inter-trial interval (ITI) between trials, and during this interval the experimental chamber stops operating typically for several seconds.

Blough and Blough (1977) suggested that this method can minimise having difficulties in gaining a stable baseline from the conditioned suppression method, and minimises the risk of having excessive responses on the manipulandum during the absence of the S^D under the one lever method. The yes-no method was used successfully with possums in an auditory study conducted by Signal et al. (2001), and is deemed to be the best method to apply to measure the auditory ability of brushtail possums in the current research.

Stimulus Presentation

There are two main ways of presenting stimulus to an animal, one is the method of constant stimuli and the other one is the method of limits. In the method of constant stimuli, the animal is presented with five to six predetermined

stimuli that varied in intensity in a randomised order (Stebbins, 1970). The problem with this method is that the testing stimuli have to be chosen before the experimental sessions begin without having any knowledge of what the animal can detect. Thus this can be inefficient if the chosen stimuli might always be detected or might never be detected by the animal.

The method of limits was described by Stebbins (1970), in which a presenting stimulus is initially chosen randomly at a stimulus intensity which can always (or never) be detected by an animal. The intensity is then either increased (ascending) or decreased (descending) over the following trials, depending on the starting point, until reaching the intensity where the animal can (or cannot) detect the stimuli.

The method of limits is considered as a more efficient method than the method of constant stimuli (Stebbins, 1970), because the intensity of the stimuli in the following trial is determined by an animal's performance in the current trial. For example, if a stimulus is presented in a descending order and the animal detects the stimulus in the current trial, then the stimulus intensity in the next trial decreases. In an ascending order condition, if the animal does not detect the stimulus in the current trial, then the intensity of stimulus is increased for the next trial. A problem with this method is a sequence effect, in which an animal tends to exhibit high thresholds when a stimulus is presented in an ascending order; or low thresholds when the stimulus is presented in a descending order (Stebbins, 1970). This can occur simply because an animal will tend to continue responding on a yes manipulandum in descending trials beyond thresholds, and the reverse (responding on a no manipulandum) during ascending trials.

A procedure, using blocks of trials, is a variation of the method of limits that has successfully been used to reduce the sequence effect because the intensity of the stimulus is not decreased or increased on every trial (Loop, Petuchowski & Smith, 1980; Signal, 2001). In a block of trials, a set number of stimulus-on (with a certain intensity) and -off trials is randomly presented to an animal, if the animal makes over a certain percentage of correct responses in the block, the stimulus intensity of on trials will be decreased for the next block of trials.

This was the method Signal et al. (2001) used to measure the auditory threshold of brushtail possums at 880 Hz. Each block contained 10 stimulus-on and 10 -off trials. Initially the volume was set at 80 dB (A), and if a brushtail possum responded correctly on 50% or more of the block, the intensity was decreased by 8 dB (A) for the following block. This continued until the possum responded correctly on fewer than 50% of 20 mixed on and off trials in a block. Signal et al. (2001) successfully found the minimum volume required for the brushtail possums to detect a sound (at 880 Hz) using this method. It seems that using blocks of trials is the best way to present stimuli for the current study to measure the hearing ability of possums.

Data Analysis

Classical Psychophysics and a Concept of Absolute Threshold

Signal et al. (2001) used the concept of a threshold to measure the auditory ability of possums using a tone of 880 Hz. Fechner in 1860 first came up with an idea that later developed as a concept of “sensory threshold” that was either the minimum perceptible stimulus strength (the absolute threshold) or the minimum perceptible difference in the intensity of the two stimuli (the differential threshold: Green & Swets, 1966; McCarthy, 1981; Swets; 1996).

During a psychophysical experiment, an animal is typically presented with a stimulus varied in intensity (e.g., the decibel (dB (A)) in the sound measure), and the animal's correct detections of both the presence and absence of a stimulus are reinforced. The animal's performances (the proportion of correct detections) in the presence of a variety of different stimulus intensities can be plotted against the measurement of stimulus intensity, and this is called a psychometric function (Green & Swets, 1966; Swets; 1996). Engen (1972) pointed out that according to the concept of the absolute threshold, the psychometric function should be a step-like function, in which, as the stimulus intensity increases, the proportion of correct detection remains at 0 (no detection at all) until, suddenly, the proportion moves up to 1 (a perfect detection). As Engen (1972), Green and Swets (1966) and Swets (1996) have reported many psychometric functions have commonly been found to be ogival in a form rather than step-like. This means that the proportion of correct detection gradually increases as the stimulus intensity increases. For example, when a tone gets louder, an animal detects the tone more accurately. The threshold is often regarded to be at the stimulus intensity where the animal detects the stimulus correctly 50% of the stimulus-on trials, or 75% of overall trials that includes both stimulus-on and -off trials (Blough & Blough, 1977; Green & Swets, 1966; Swets; 1996; Treutwein, 1995). According to Signal (2002) and DeMello (1989), it was considered that using the threshold level of 75% of overall trials should theoretically be the same as using the threshold level of 50% of the stimulus-on trials only. This is based on the idea that an animal should have performed with 100% accuracy on the stimulus-off trials regardless of the stimulus intensity in the on trials. The animal's ability to discriminate stimulus should deteriorate only during the stimulus-on trials relative to the

strength of a stimulus. However, Signal (2002) and DeMello (1989) found that the proportion of animal's correct responses deteriorated in both -on and -off trials as the stimulus intensity was weakened.

Signal Detection Theory (SDT)

Another approach to study the sensory ability of animals is based on signal detection theory (SDT). SDT is based on the idea that an observer perceives an 'input' and the observer determines if the input contains a signal or not (s + n or n only: Green and Swets, 1966; Swets, 1996). Unlike the absolute threshold, which includes the concept of a fixed threshold, within SDT, it is considered that the observer's decision depends on a decision criterion (Blough & Blough, 1977; Green & Swets, 1966; McCarthy, 1981; Swets, 1996). The decision criterion is influenced by the observer's past experience and the "payoff" or predicted consequence for their responses (Blough & Blough, 1977; Green & Swets, 1966; McCarthy, 1981; Swets, 1996). A "strict" criterion would imply that the observer (or the animal) responds to a 'yes' manipulandum at quite high intensities, giving a high threshold. In contrast, a "lax" criterion would give a low threshold measures.

Stimulus Response Matrix

In yes-no procedures, the responses that animals make can be categorised into four different types that are illustrated in the stimulus response matrix (Figure 1). Hits (*W*) occur when animals respond on the 'yes' manipulandum during stimulus-on (s + n) trials. Correct rejections (*Z*) occur when the animals respond during the 'no' manipulandum on stimulus-off (n) trials. Misses (*X*) occur when the animals respond on the no manipulandum during stimulus-on trials. False

Response

Stimulus	Yes	No
Noise + signal	*W* Correct response (Hit) P (yes / s + n) (i.e., P = 0.75)	*X* Incorrect response (Miss) P (no / s + n) (i.e., P = 0.25)
Noise	*Y* Incorrect response (False Alarm) P (yes / n) (i.e., P = 0.25)	*Z* Correct response (Correct Rejection) P (no / n) (i.e., P = 0.75)

Figure1. Stimulus response matrix; all response type in yes-no procedures.

alarms (*Y*) occur when the animals respond on the 'yes' manipulandum during stimulus-off trials.

According to Green and Swets (1966) and Swets (1996), if an animal is presented with stimulus-on trials 100 times, and if the animal responded on the yes manipulandum 75 times and on the no munipulandum 25 times, then the proportion of hits or P (yes / s + n) during on trials will be 0.75 (Green & Swets, 1966). Similarly if the animal is presented with 100 stimulus-off trials, and if the animal responded on the no manipulandum 75 times and on the yes manipulandum 25 times, then the proportion of false alarms on noise only trials, P (yes / n), will be 0.25, and these add up to 1.0 (Green & Swets, 1966). Data are often plotted with P (yes / s + n) on the y-axis and P (yes / n) on the x-axis. Such plots are known as a receiver operating characteristic (ROC) graph.

d' in SDT and log d in Generalised Matching Law (GML)

In SDT, a parameter *d'* presents the observer's sensitivity towards the difference between two stimuli, n and s + n (Green & Swets, 1966; Swets, 1996). If *d'* equals zero, the proportion of hits (*W*) and false alarms (*Y*) are equal. This means that the animal made the same number of responses on the yes and no manipulandum during stimulus-on and -off trials (detected s + n 50% of the stimulus-on trials). In this case, it is considered that the animal was unable to discriminate between s + n and n, or made responses at or below a chance level. A larger *d'* value means the animal discriminated the two stimuli better (Green & Swets, 1966; Swets, 1996).

Davison and Tustin (1978), Davison and McCarthy (1988) and Nevin (1969) suggested that yes-no procedures can be considered as concurrent schedules of reinforcement with added stimuli. Under concurrent schedules of reinforcement,

an animal responds on one of the two simultaneously available but incompatible manipulanda, each of which is associated with a different schedule of reinforcement (Baum, 1974). The distribution of responses on each of the two manipulanda depends on the schedules of reinforcement (i.e., the relationship between stimuli, response and reinforcers), the reinforcement history of the animal, and any inherent and position bias (Baum, 1974; McCarthy, 1983). The inherent biases are the constant preferences towards one manipulandum over another (Baum, 1974; McCarthy, 1983).

Davison and Tustin (1978) pointed out that similar features to concurrent schedules of reinforcement could be seen in yes-no procedures. First, two response manipulanda are concurrently available for an animal to respond on. Then, in the presence of a stimulus (s + n), responding on one of the manipulanda (on a yes key) will be followed by a delivery of reinforcer (i.e., food), and in the absence of the stimulus (n only), responding on the other (on a no key) will be followed by reinforcer. If the two stimuli (s + n and n) are indistinguishable, the animal's response on the yes or no keys depends heavily on the schedules of reinforcement and any inherent biases. As the two stimuli become more distinguishable, responding on the yes key increases during the stimulus-on trials (s + n) and responding on the no key increases during the stimulus-off or n only trials (Davison & Tustin, 1978).

Davison and Tustin (1978) developed the behavioural detection model to conceptualise data gathered from the yes-no procedure of sensory detection tasks. The model is based on the generalised matching law (GML), which was first used to describe the data collected from concurrent schedules of reinforcement by Baum, (1974) and Staddon (1968; Davison & McCarthy, 1988). Their model

treated the tendency to respond differently on the two manipulanda in the two trial types as a biaser in the generalised matching law (GML). That is, there would be a bias toward one response during stimulus-on trials and to the other during stimulus-off trials. Equation 1 and 2 assume this bias is the same size in both trials and so more responses towards the yes key on stimulus-on trials (+ log *d*) and away from the yes key on stimulus-off trials (– log *d*). The equation for the stimulus-on trials is;

$$\log (B_W / B_X) = a \log (R_W / R_Z) + \log c + \log d \quad (1),$$

and for the stimulus-off trials is;

$$\log (B_Y / B_Z) = a \log (R_W / R_Z) + \log c - \log d \quad (2),$$

where B is the number of responses made, and R is the number of reinforcer gained in each stimulus-on and -off trials in a session. The subscripts $_W$, $_X$, $_Y$ and $_Z$ refer to the stimulus response matrix in Figure 1. The parameter *a* (the sensitivity to reinforcement) was suggested by Davison and Tustin (1987) to be the same under both stimulus-on and -off condition. For example, variables such as reinforcement rates are normally kept as constant as possible between the two manipulanda through experimental sessions (McCarthy, 1981).

Log *c* represents any inherent biases towards one manipulandum over another, and this is independent from stimulus discriminability (Davison & McCarthy, 1988; McCarthy, 1981; Davison & Tustin, 1987). Davison and Tustin (1987) derived log *c* by adding Equations (1) and (2) and assuming that the reinforcement rates in both conditions are equal so that R_W=R_Z, and log(R_W/R_Z) equals zero,

$$\log c = 0.5 (\log (B_W / B_X) + \log (B_Y / B_Z)) \quad (3).$$

Log *d* is different from *d'* in SDT but is a related measure (Davison & Tustin, 1978; McCarthy & Davison, 1980). Log *d* is the discriminability of two stimuli, s + n and n alone, and excludes any unwanted biases, log *c*, such as inherent and position biases which might be a part of an animal's response (McCarthy & Davison, 1980). Log *d* can be derived by subtracting equation (2) from (1), only when sensitivities to reinforcement are equal which Davison and Tustin (1978) showed to be the case or when log (R_W / R_Z) is zero,

$$\log d = 0.5 (\log (B_W / B_X) - \log (B_Y / B_Z)) \quad (4).$$

Davison and Tustin (1978) rearranged Equation (4);

$$\log d = 0.5 \log (B_W \cdot B_Z / B_X \cdot B_Y) \quad (5).$$

When the animal detects a stimulus well, then the value of log *d* is larger. When the animal detects the stimulus at a chance level (50% of overall trials), log *d* equals 0 (Davison & McCarthy, 1988). The minimum detectable stimulus intensity determined from the threshold study using 75% response accuracy level in overall trials would be equivalent to the intensity at the log *d* value of 0.48 (DeMello, 1992; Signal, 2002).

A Behavioural study on Brushtail Possums Auditory Ability

Signal (2002), as previously mentioned, investigated the auditory ability of six brushtail possums using a yes-no procedure. She trained six possums with one tone intensity then reduced the intensity over blocks of trials. She presented the data using both *d'* and log *d*.

Signal (2002) found that as the tone intensity decreased over blocks of trials, the percentage correct for both tone-on and tone-off trials reduced, and the percentage correct for tone-on trials reduced more rapidly than that from tone-off trials. Signal (2002) reported sound intensities that gave 75% correct and that

gave log *d* of 0.48 were similar across all six possums, and similarly the sound intensities that gave 50% correct and that gave log *d* of 0 were the similar for all six possums.

One of Signal's (2002) concerns was that, in her study, the background noise in the communal environment where other possums were kept in individual cages during and outside of the experimental sessions might have affected the possums' performance in the discrimination tasks. To test this, she conducted threshold sessions with one of the possums in a sound-attenuated chamber. She compared the results with those gained in a communal environment. The results showed that the possum's performances in the communal environment and in a sound attenuated chamber were similar. She concluded that there is no need to conduct this experiment in an isolated chamber.

Signal (2002) suggested that it would be possible to determine a full audiogram of the brushtail possums using the same procedure. The full audiogram is a graph in which an organism's minimum perceptible volumes (dB (A)) are plotted against the different frequency of the sounds in Hz (e.g., Aitkin, Bush, & Gates, 1978; Aitkin, Gates & Kenyon, 1979; Ravizza, Heffner & Masterton, 1969; Temple, Foster & O'Donnell, 1984).

Summary

So far, only one study (Signal et al., 2002) has investigated the auditory ability of brushtail possums (*Trichosurus Vulpecula*) behaviourally, and thus more research is needed. Determining the audiogram of the possums will give us a better understanding of their hearing abilities and could potentially help to improve the current trapping methods. For example, Carey, O'Connor, Mc Donald and Matthews (1997) suggested adding an auditory lure to a standard bait

station may attract possums to the bait station. The audiogram of a possums would, at first, give some limits for the intensity and frequency or frequencies in any such lures.

The purpose of the current study was to replicate and extend Signal's (2002) study. This involved investigation of the auditory ability of the brushtail possums at 880 Hz using a yes-no procedure with blocks of trials. Then, the auditory ability of the possums across different frequencies (Hz) was investigated and the data were presented on an audiogram.

METHOD

Subjects

A total of 9 mature brushtail possums *(Trichosurus Vulpecula)* served as subjects. Their details are summarised in Table 1. There were a total of five female possums named Caper, Kimmy, Lexi, Olive and Sammy, and four male possums named Mickey, Mouse, Peppi and Wembley.

Caper, Mickey and Sammy were born in captivity. Kimmy, Lexi and Olive were captured as juveniles. Mouse was captured in his adulthood. Peppi and Wembley were both found in their dead mothers' pouches in 2006 and were hand reared.

At the beginning of the current study, Peppi and Wembley were 1-year-old, Caper was 1.5-years-old, Sammy was 2.5-years-old, Olive was 3-years-old, Kimmy and Lexi were 3.5-year-olds, and Mickey was 8.5-years-old. The estimated age of Mouse was 4 years at the beginning of this study.

Caper, Mouse, Peppi, Sammy and Wembley were experimentally naïve. Kimmy, Lexi, Mickey and Olive had previous experiences in performing on visual discrimination tasks. Mickey had also performed on Fixed Ratio (FR) schedules of reinforcement and concurrent schedules of reinforcement.

Kimmy died from a twisted intestine, Lexi's death was caused by a fur ball in her intestine, and Sammy died as a result of bladder stone before completing this experimental study. Olive, Peppi and Wembley replaced these three possums part way through the study.

Supplementary feed of dock leaves and apples (or carrot), were given to every possums daily. Possum food pellets, which were specially manufactured by Camtech

Table 1.

Details of Each Subject; Name, Age, Gender and Historical Exposure to experiments.

Name	Age (years)	Gender	Previous exposure to experiments
Sammy	2.5	Female	-
Olive	3.0	Female	Visual discrimination tasks
Caper	1.5	Female	-
Kimmy	3.5	Female	Visual discrimination tasks
Wembley	1.0	Male	-
Lexi	3.5	Female	Visual discrimination tasks
Peppi	1.0	Male	-
Mickey	8.5	Male	Visual discrimination tasks, FR schedules of reinforcement, and the concurrent schedules of reinforcement
Mouse	4.0	Male	-

Nutrition Ltd., were provided in the morning when no experimental session was conducted. Possums were weighed fortnightly, and the amount of supplementary feed and possum pellets for each possum was adjusted according to the possums' weight. Water was available at all times.

On the days when a session was conducted, if a possum had gained fewer than 10 reinforcers during a session, a post–feed of pellets was provided for the possum to maintain their weight. In this case, 20 to 30 g of possum pellets, depending on the number of reinforcers the possum earned in the session and its weight, was given. Sammy was always given a post-feed of mash, a mixture of 20 g possum pellets and approximately 40 ml of sugary water (two table spoons of sugar were dissolved into 1,500 ml water). When she earned fewer than 10 reinforcers, in which case her daily mash was increased to 30 g pellets and 60 ml sugar water.

Apparatus

The possum communal room, in which the possums were kept, was also used as an experimental room. Figure 2 shows this experimental room, the picture was taken from the entrance door aimed towards the end of the room. The experimental room in was under a 12 hr/12 hr reversed day/night cycle. During the day phase, three white light bulbs (100 W) were illuminated, and three red light bulbs (60 W) were lit during the night phases. A fan situated on the left wall and an electric heater were used to help maintain a constant temperature (between 15 and 25 C°). The fan was turned off during the experimental sessions to minimise the noise that might affect the performance of the possums during sessions.

Figure 2. A picture of the possums experimental room (A), and pictures of the experimental response panel taken from the back (B) and the front (C) for a possum.

Each possum was kept in an individual metal wire cage (860 mm X 510 mm X 540 mm) as shown in Figure 2. The possums were housed in the order of Sammy (or Olive), Caper, Wembley (or Kimmy), Peppi (or Lexi), Mickey and Mouse, with Sammy in the cage closest to the door. There was 50 mm gap between the cages. A wire shelf was situated 250 mm from the top of each cage. A waterspout was attached to the front top corner of each cage. A nest box made of plywood (355 mm X 455 mm X 200 mm) was attached to the top of each cage. Each possum had access to its nest box (from the cage) through a hole (220 mm X 120 mm). Attached to the front of each cage was a plywood door (550 mm X 330 mm). To the right of the door, there was a rectangular hole (104 mm X 44 mm) through which a metal feed tray (100 mm X 36 mm X 146 mm) could be inserted.

All experimental sessions were conducted in the individual cages. Figure 2 and 3 show pictures and a diagram of an experimental response panel. A magazine (195 mm X 112 mm X 231 mm) was attached to the centre of the plywood door, could be raised to allow a possum to access to the food through a magazine access hole (30 mm X 30 mm). A stiff wire was attached across the middle of the magazine access hole for some possums to prevent them reaching the food with their paws at times when the magazine was not operated. Magazines for all possums, except for Sammy, contained a mixture of steamed-flaked barley and cocoa puffs (a ratio of 15:1 by volume). A mixture of rolled oats, cocoa puffs and sunflower seeds (a ratio of 10:1:1 by volume) was used for Sammy only.

Each response panel contained three holes (6 mm in diameters) to insert response levers (250 mm length) above the magazine. The minimum force required to depress

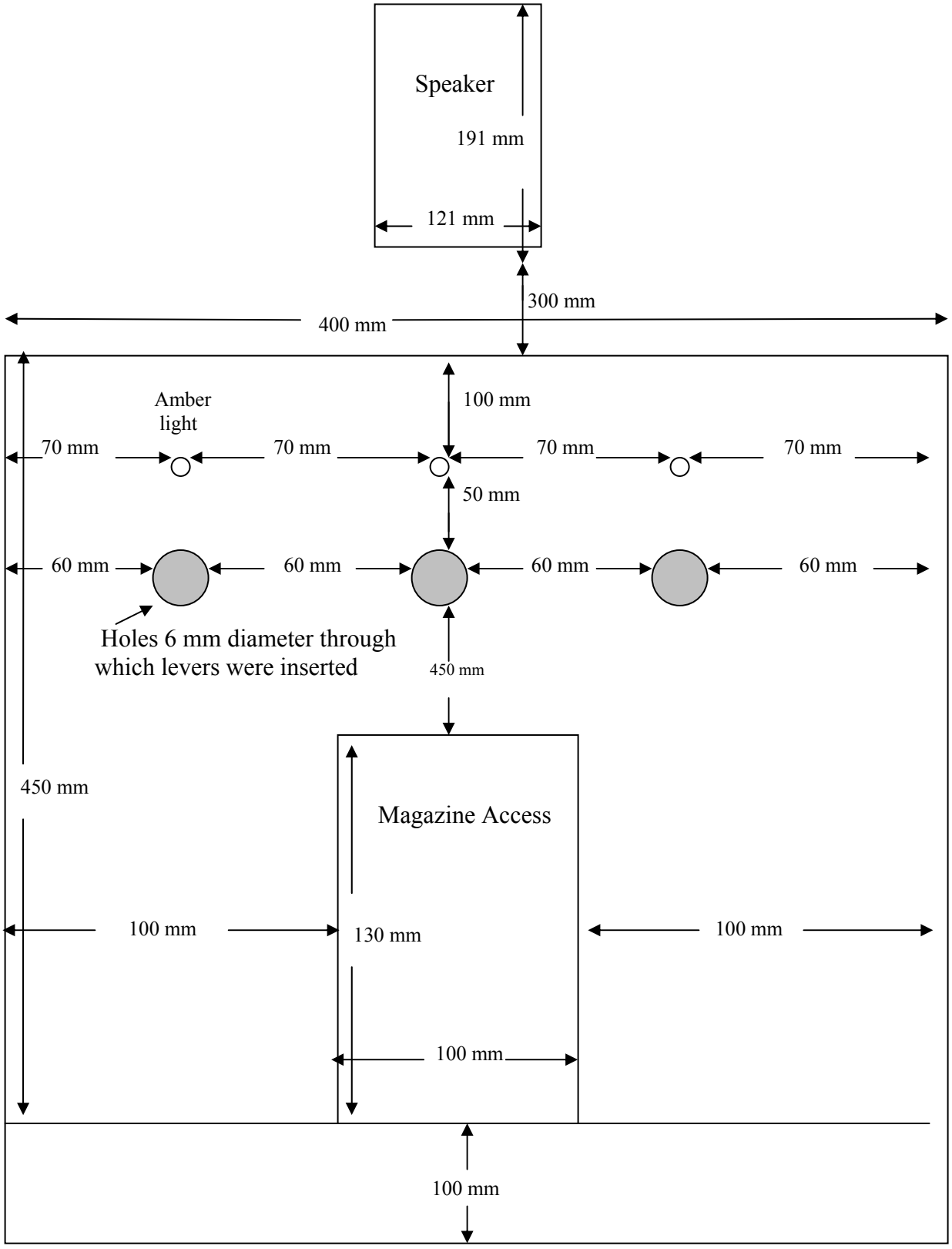

Figure 3. The diagram of the experimental response panel situated in the individual cage.

each of the lever was 0.25 N. An amber light (LED, 2.1V, 590 nm, Toshiba TLYH157P) was placed 50 mm above each lever. A Flying Lead Piezo Sounder (ABI 006-Piezo Indicator) measuring 20 mm in diameter was attached to the back of the response panel, 9 cm from the left and 50 mm below from the edge of the response panel. The sounder provided possums with an auditory feedback, a 0.05-s beep (at 90 dB (A) at 3.7 kHz) when possums responded on a side lever correctly.

Two different types of speakers (Digitor indoor/outdoor speakers; A977; and Foster ribbon tweeters) were used to play auditory stimuli at different frequencies (see Appendix A for more information on which type of speaker was used for which frequencies and why). The Digitor speakers were used to produce sounds between 100 Hz to 10 kHz, modified Digitor speakers were used to play tones at 12.5 and 15 kHz, the tweeters were used to produce tones at 15 kHz and over. Either the speaker or the tweeter was set 100 mm above the central light for each possum.

An oscilloscope (Kikusui 40 MHz COS 5040^{TM}), a multi-meter (Fluke 79 series, manufactured by John Fluke), and a microphone (Sennheiser 21/22, a frequency range between 20 to 20000 Hz), or the tweeter or speaker (used as a microphone) were used to test each tone frequency to make sure each speaker was producing the tones accurately (see the measuring procedure in Appendix A).

A sound pressure meter (Testo 816) that could measure sounds between 30 and 130 dB(A) was used to assess tone intensity and, if necessary, to adjust it (see more detail in Appendix B). At the tones 20 kHz and over, a calibrating procedure was used to adjust tone intensity, with this, due to the limitation of the sound pressure meter the tone intensity was set at 7 kHz before the trial frequency was set (see Appendix B).

All experimental and training conditions were controlled by a computer (Dell Optiplex GX110), using the MED PC ™ IV, software and an interface in which the programmable audio generator (ANL-926) was inserted. The specifications of the programmable audio generator allowed for produce of tones between 10 and 35000 Hz, and was most functional between 20 to 100 dB(A). The interface was attached to a PA amplifier manufactured by Toa™ (later replaced with Yamaha AX-890, due to the PA amplifier was producing static noise at higher frequencies) to control the sound frequency and pressure. The amplifier was connected through a latching relay to each speaker to be able to play sound from one speaker at a time.

All data were stored by the computer and were also recorded daily in a data book.

Procedure

Each session was conducted for possums five to seven mornings a week during the possums' night phase, approximately 2 hr into the night phase. All possums were exposed to a series of training and experimental conditions.

Training Conditions

There were three different types of training, lever pressing training, and side lever training with and without prompts. In this section, the trainings with initial six possums (Sammy, Caper, Kimmy, Lexi, Mickey and Mouse) with a tone frequency of 880 Hz are described. The same training procedures except using different tone frequencies were used for the other possums, depending on which frequency Sammy, Kimmy and Lexi were testing on when they died. Olive was trained with a 2 kHz tone, while Peppi and Wembley were trained with a 4 kHz tone.

Each training session lasted for 40 min, or it was terminated if a possum gained 100 reinforcers during a session.

Lever Pressing Training. At the beginning of each session of this training, only the central lever was put in place. While the central light was illuminated, every effective lever press, which would operate an auditory feedback and terminate of the central light lit, was always followed by a 3-s access to the reinforcer and then a 3-s inter-trial interval (ITI) before the next trial began. During the ITI, all lights were turned off, and the stimulus, manipulanda and the magazine stopped operating. This procedure that a reinforcer is delivered after every effective response is typically called a Fixed Ratio (FR) 1 schedule of reinforcement.

An extra training was provided to the experimentally naïve possums by using the method of successive approximations to the desired response. In this method, while the central light was illuminated, the possum's existing behaviour was gradually changed to a desired, target, behaviour (i.e., the effective lever pressing) across consecutive trials by delivering reinforcers for successive approximation to the desired response. For example, a reinforcer was delivered when a possum faced the central lever, then when it moved closer to the central lever, the possum finally made an effective lever pressing. Possums with previous experiences in performing on experimental tasks did not require this extra training.

Once all possums were pressing the lever consistently (i.e., 100 times within 40 min for at least three consecutive sessions), and then the next training, side lever training with prompts, began.

Side Lever Training with Prompts. At the beginning of each session in this training, all three levers were inserted. In the first phase, there were left and right light trials, and no tone was presented (Figure 4). Each trial was presented pseudo-randomly using a version of the Gellerman series (1933), ensuring there would be approximately equal numbers of left and right trials in a session and no more than three consecutive trials of one type. At the beginning of both trial types, the central light was lit, and responding on the central lever resulted in the termination of central light and the illumination of one of the side lights. A response to a side lever under the lit light resulted in a feedback beep. Correct responses were reinforced under a Variable Ratio (VR) 1.5 schedule of reinforcement across trials in a session (a reinforcer, 3-s access to food, was delivered to the possum after it made, on average, 1.5 correct responses) with the combination of a version of the Gelleman series (1993). Under this procedure, the VR 1.5 schedule of reinforcement was independently programmed on the left and right lever, separately. At the beginning of each trial either a left or right correct response was also nominated pseudo-randomly to be effective for a delivery of reinforcement (if the variable-ratio requirement was satisfied). For example, if the possum made a correct response in the nominated trial, and if the reinforcer was due to be delivered under the VR 1.5 schedule of reinforcement, then a reinforcer was delivered. If the presented trial was not nominated for delivering of reinforcement, or if there was insufficient number of correct response after completion of the current trial, then the reinforcer was not delivered.

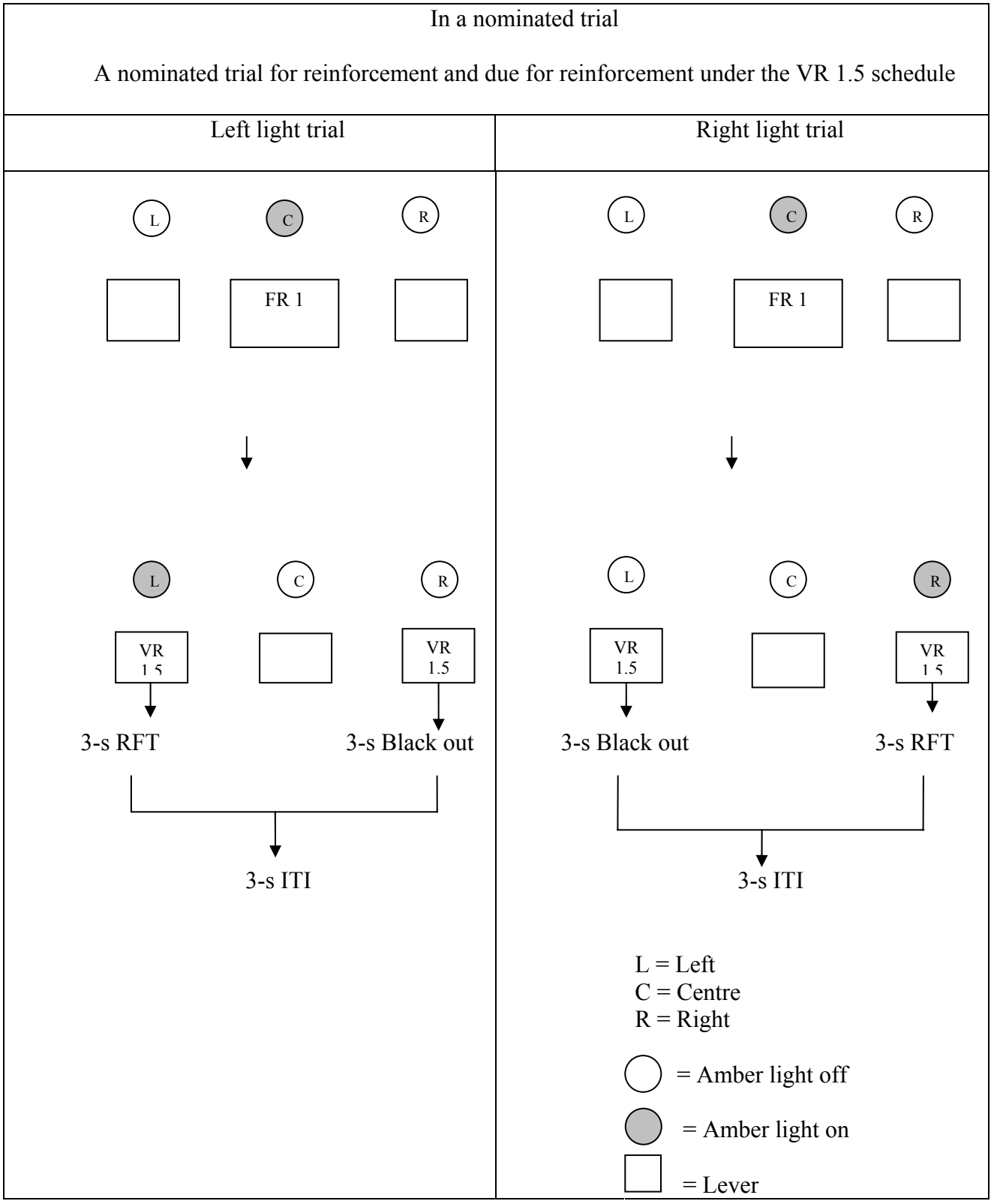

Figure 4. Diagrams of the left and right light trials in the side lever raining with prompts.

Responding to the lever under the unlit light was always resulted in the termination of the side light, no feedback beep, a 3-s blackout period, and then a 3-s ITI before the next trial began.

During this training, each possum started their session at a different time of the day to prevent the sound presented for one possum affecting the performance of the other possum. Each possum initially started their session with a 20 min delay after the previous possum started, and later the duration of delay increased to 30 min and then 40 min. At the time when the delay increased to 40 min, no sessions overlapped, and each session was conducted sequentially from Sammy (or Olive), then Caper, Kimmy (or Wembley), Lexi (or Peppi), Mickey and then Mouse. This order was later changed to Mickey, Mouse, Sammy (or Olive), Caper, Kimmy (or Wembley), and then Lexi (or Peppi) after Mickey stopped responding with this order, and to increase the interval between the end of his experimental session and his afternoon feed.

The second phase of the training (five sessions) involved the introduction of tone-on and tone-off trials. The procedure remained the same except for the right correct trial a tone (880 Hz at 80 dB(A)) sounded when the central lever was pressed until one of the side levers was pressed. Left correct trials remained as the same. To prevent the sound has been played continuously, an abort procedure was introduced. In this, a trial (tone-on or -off) would be aborted (all lights were turned off, and in tone-on trials, the sound would also be terminated) when no response was made on a side lever after 1 min since the central lever response. The abort was followed by a 3-s black out and then a 3-s ITI before the next trial began.

Side Lever Training without Prompts. This training was very similar to the second phase of the side lever training with prompts. The only difference was that both left and right lights were lit following the response to the central lever during both tone-on and -off trials. Over the first 20 sessions, the VR schedule was increased from VR 1.5, to VR 2.5 and then VR 4.6.

During this training procedure, Kimmy, Lexi and Mickey responded correctly approximately at 50%, while the other possums (Sammy, Caper and Mouse) responded with over 90% accuracy. At this point the data were analysed to assess the differences in the behaviour of these two groups of the possums. The results, which are presented in the Results section, showed that Kimmy, Lexi and Mickey had shorter response latencies to the side levers, compared to the other group of possums. As a result of this, the stimulus (tone or no tone) presented duration was shorter for Kimmy, Lexi and Mickey than it was for the other possums. To increase the duration of the stimuli presentation, an FR 5 schedule was introduced to the central lever. This final training procedure with the FR 5 schedule was is presented diagrammatically in Figure 5. Under the FR 5 schedule, all possums were required to press the central lever five times before the side lights lit up. While possums were pressing the central lever, the central light was illuminated and the stimulus was presented if it was a tone-on trial. The fifth lever press on the central lever turned off the central light and illuminated the side lights. Responding on either of the side levers turned off the side lights and terminated the stimulus presentation. Therefore all possums were exposed to the stimuli for a longer period of time with the FR 5 schedule.

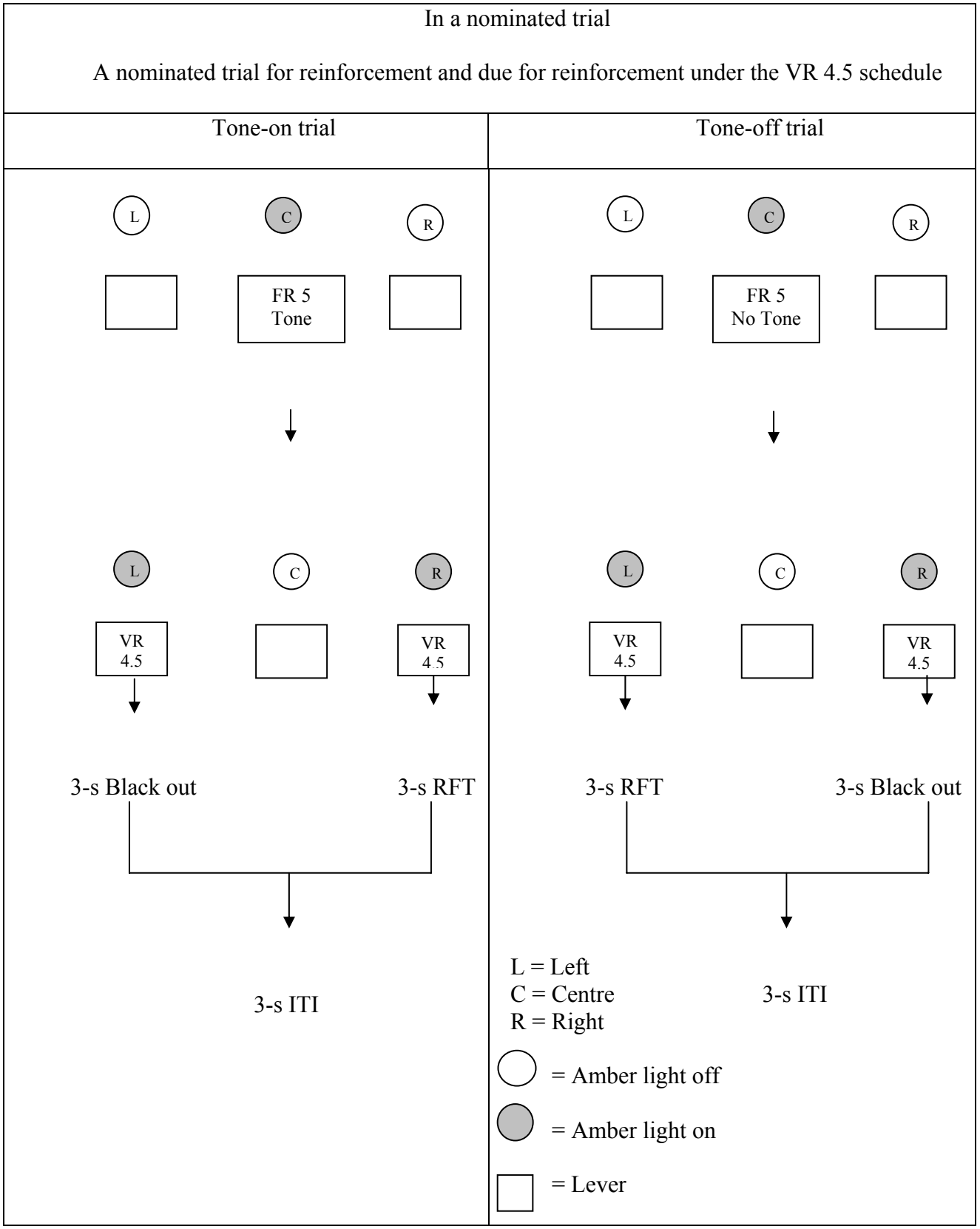

Figure 5. Diagrams of the tone-on and tone-off trial in the final procedure of the side lever training without prompt.

Once the FR 5 schedule was introduced, Kimmy, Lexi and Mickey increased their response accuracy to 90% or over. At this point, all series in the training condition were deemed to be completed.

Subsequently, in the training condition for new possums (Olive, Peppi and Wembley), the FR 5 was always used for the trials which involved stimulus (tone-on and -off) presentations.

Experimental Condition

The experimental condition consisted of two different types of sessions, the final procedure of the training without prompt and then probe sessions. At the beginning of each experimental condition, the tone frequency was changed for the condition and the volume was set at 80 dB(A) (or 72 dB(A) at 15 and 20 kHz conditions; see more detail in Appendix B) for tone-on trials. The probe sessions were started when a possum achieved 90% or more correct (and 85% or more for Mickey and Mouse at 30 and 35 kHz; see more detail in Appendix C) for five consecutive sessions. When the training was completed, at least five probe sessions were conducted for each possum. Figure 6 shows the diagram of a probe session. The probe session contained several blocks, in which 20 mixed tone-on and -off trials were arranged pseudo randomly using a version from the Gellerman series (1933). The probe session started with a block in which the tone was set at 80 dB(A) (or at 72 dB(A) in 15 and 20 kHz Condition, or at 64 dB(A) between third and fifth probe sessions in 12.5 kHz condition for Mouse; for more details see Appendix B and C) for the tone-on trials. If the possum responded correctly on 60% or more of the block (or 50% in the first condition at 880 Hz and some of the second condition at 2 kHz for those possums that completed trials at this frequency), then the

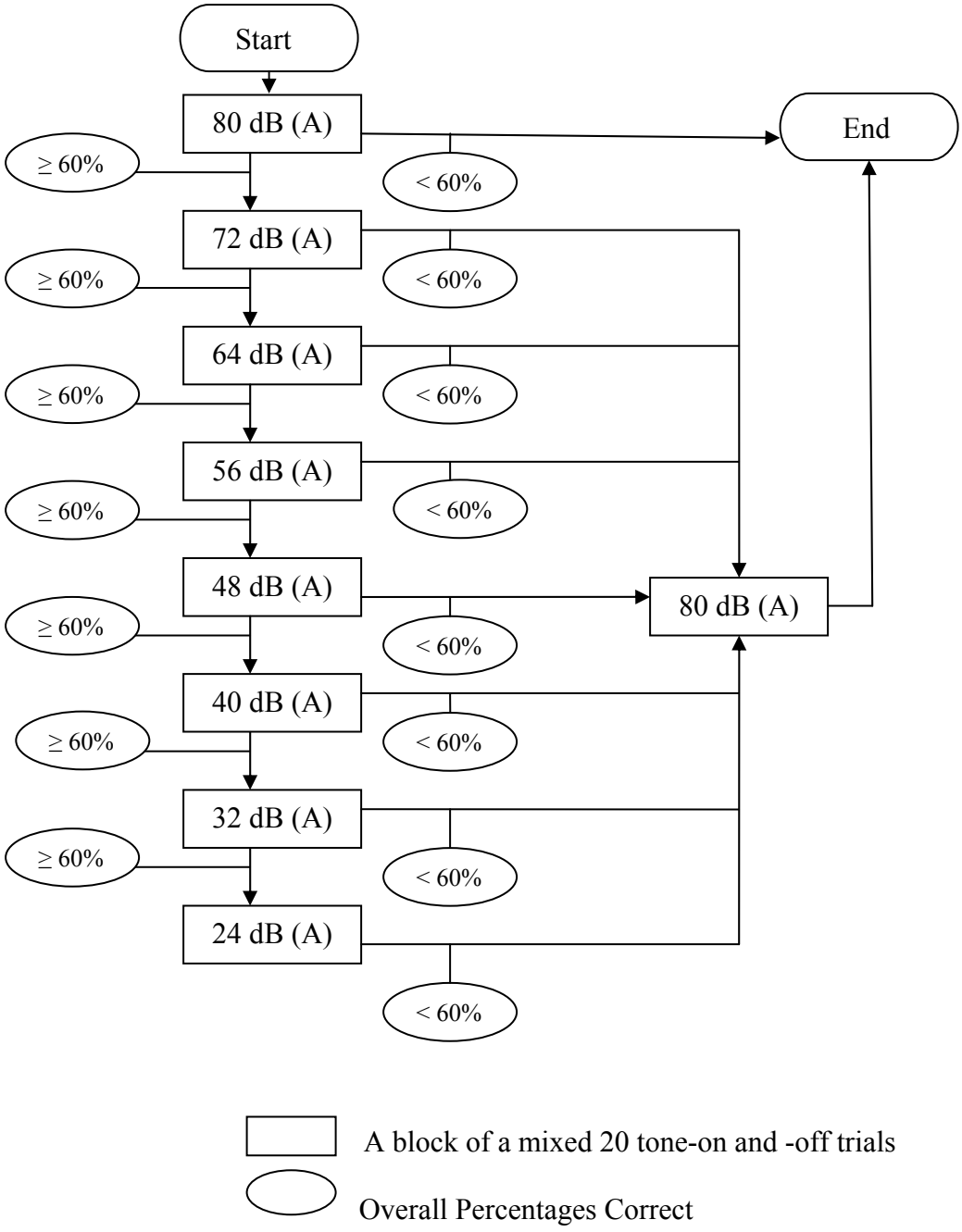

Figure 6. A flowchart of a probe session starting at 80 dB(A) and with the cut-off criterions of either that possums completed a block at 24 dB(A) or that the possum within a block with lower than 60% accuracy.

volume was reduced by 8 dB(A) for the next block. If the possum responded below 60% (or 50%) in this block, then the probe session was discontinued. If the possum responded correctly on 60% or more (or 50% or more) of the trials in the next block, then the intensity was again reduced by a further 8 dB(A) for the following block. The volume continued to be reduced across the blocks until reaching a cut-off criterion of which the possum responded to less than 60% (or 50%) of trials correctly in a block, or until it completed a block at 24 dB(A) or 0 dB(A; between 880 and 15 kHz condition for Sammy, Wembley, Peppi, Mickey and Mouse; and between 880 to the part way though of 15 kHz for Caper). At this point, the possum was moved to the final block of trials in which the intensity of the tone was returned to the initial tone intensity (either 64, 72 or 80 dB(A)). A successful probe session occurred when the possum responded 80% or more of the trials correctly in both the first and the last blocks, and was completed within 60 min.

Between probe sessions, at least one training session had to be conducted, and the percentage of correct responses in the training session had to be 90% or over (or 85% or over for Mickey and Mouse for 30 and 35 kHz) to be able to conduct a probe in the following session. If the possum did not achieve this, another training session followed. This continued until the possum reached the criterions in a training session. At the first three conditions at 880 Hz, 2 and 4 kHz, after all possums completed five probe sessions (or after the third condition at 4 kHz, once an individual possum completed all five probe sessions) in an experimental condition, the next experimental condition with a different tone frequency began.

Table 2 shows the order of the experimental conditions with the different frequency tones that each possum was exposed to. The order of tone frequency was not consistent across

all possums. For Sammy, Caper, Mickey and Mouse, the tone frequency was increased from 880 Hz to 10 kHz over conditions, and then for the next condition it was reduced to 880 Hz for Sammy and Caper, and to 2 kHz for Mickey and Mouse, then for all of these possums the tone frequency was increased again from 12.5 kHz to 20 kHz across conditions for these possums, except for Sammy who died during the 12.5 kHz condition. Then for these possums except for Sammy, the tone frequency was reduced to 200 Hz, and then 100 Hz at the following conditions. After this, they were re-exposed to the 20 kHz condition, and it increased to 30 kHz then 35 kHz at the following conditions. At this point increasing the tone frequency was stopped due to the limitations with the equipment. The tone was supposed to have been reduced to below 100 Hz, and is still remained to be completed at present. As shown on Table 2, for Olive, Peppi and Wembley, the tones were not constantly increased across conditions, as they replaced Sammy, Kimmy and Lexi who had completed some conditions. These new possums started their training at the frequency which the other possums were tested at. Kimmy was only exposed to the 880 Hz condition and died during this condition. Lexi completed in the 880 Hz condition, and died during the 2 kHz condition.

Replication of Conditions. As can be seen in Table 1, a condition at 880 Hz was repeated for Sammy and Caper, and at 2 kHz for Mickey and Mouse. This is was to observe if there was any order effect or learning effect across conditions.

During the 15 kHz condition, either a modified speaker or a tweeter was used for different possums. The tweeters were used for Olive and Mouse, as these were available at the beginning of their 15 kHz condition. To make sure the possums' performance was not affected by the type of speakers used, Peppi and Wembley were again tested using

Table 2.

The Order of Experimental Conditions with Each Frequency Tone for Each Possum (kHz).

	Sammy	Olive	Caper	Kimmy	Wembley	Lexi	Peppi	Mickey	Mouse
1	0.88	2	0.88	0.88	4	0.88	4	0.88	0.88
2	2	12.5	2	-	10	2	10	2	2
3	4	15	4	-	0.88	-	0.88	4	4
4	10	20*R*	10	-	2	-	2	10	10
5	.88*R*	30	.88*R*	-	12.5	-	12.5	2*R*	2*R*
6	12.5	35	12.5	-	15	-	15	12.5	12.5
7	-	-	15	-	15*R*	-	15*R*	15	15
8	-	-	20	-	20	-	20	20	20
9	-	-	0.2	-	0.2	-	0.2	0.2	0.2
10	-	-	0.1	-	0.1	-	0.1	0.1	0.1
11	-	-	20*C*	-	20*C*	-	20*C*	20*C*	20*C*
12	-	-	30	-	30	-	30	30	30
13	-	-	35	-	35	-	35	35	35

Note. The *R* is a repeated condition, and the *C* is the repeated condition using the calibrating procedure. The first condition was where the training condition was also conducted for each possum.

the tweeters in the 15 kHz condition.

For the conditions using tones above 20 kHz, the sound intensity was adjusted by calibrating the sound frequency at 7 kHz, instead of setting the tone intensity at the testing frequency (see Appendix B). To make sure the performance of possums was not influenced by the two different procedures to adjust the intensity, the 20 kHz condition was repeated using the calibrating procedure for Caper, Wembley, Peppi, Mickey and Mouse.

RESULTS

Training Condition

The initial training consisted of lever pressing training, side-lever training with prompts and side lever training without prompts took place with the 880 Hz tone for Sammy, Caper, Kimmy, Lexi, Mickey and Mouse.

Figure 7 shows the average percentages correct for overall trials (left panel), and for tone-on and tone-off trials separately (right panel), under each training condition at 80 dB(A) plotted against sessions. Gaps between two data points are sessions where the possum did not respond at all or where equipment problems occurred during the sessions. The results show that during the side-lever training with prompts (T1), all possums responded with 90% to 100% accuracy. When the side-lever training without prompts (T2) was introduced, a decrease in response accuracy was observed for all possums. Only three possums (Sammy, Caper and Mouse) showed an increase in response accuracy to over 90% during the T2. The remaining three possums, Kimmy, Lexi and Mickey, showed no increase in the response accuracy and the remainder responded below 65% correct for overall, and tone-on and tone-off trials. At this point, latencies to the response were analysed for each possum.

Figure 8 shows average latencies to correct (On/C) and incorrect (On/IC) responses during tone-on trials, and average latencies to correct (Off/C) and incorrect (Off/IC) responses on tone-off trial during the T2 for each possum plotted against session numbers. The latency for each response type was calculated by dividing the total durations between the last response to the central lever and the

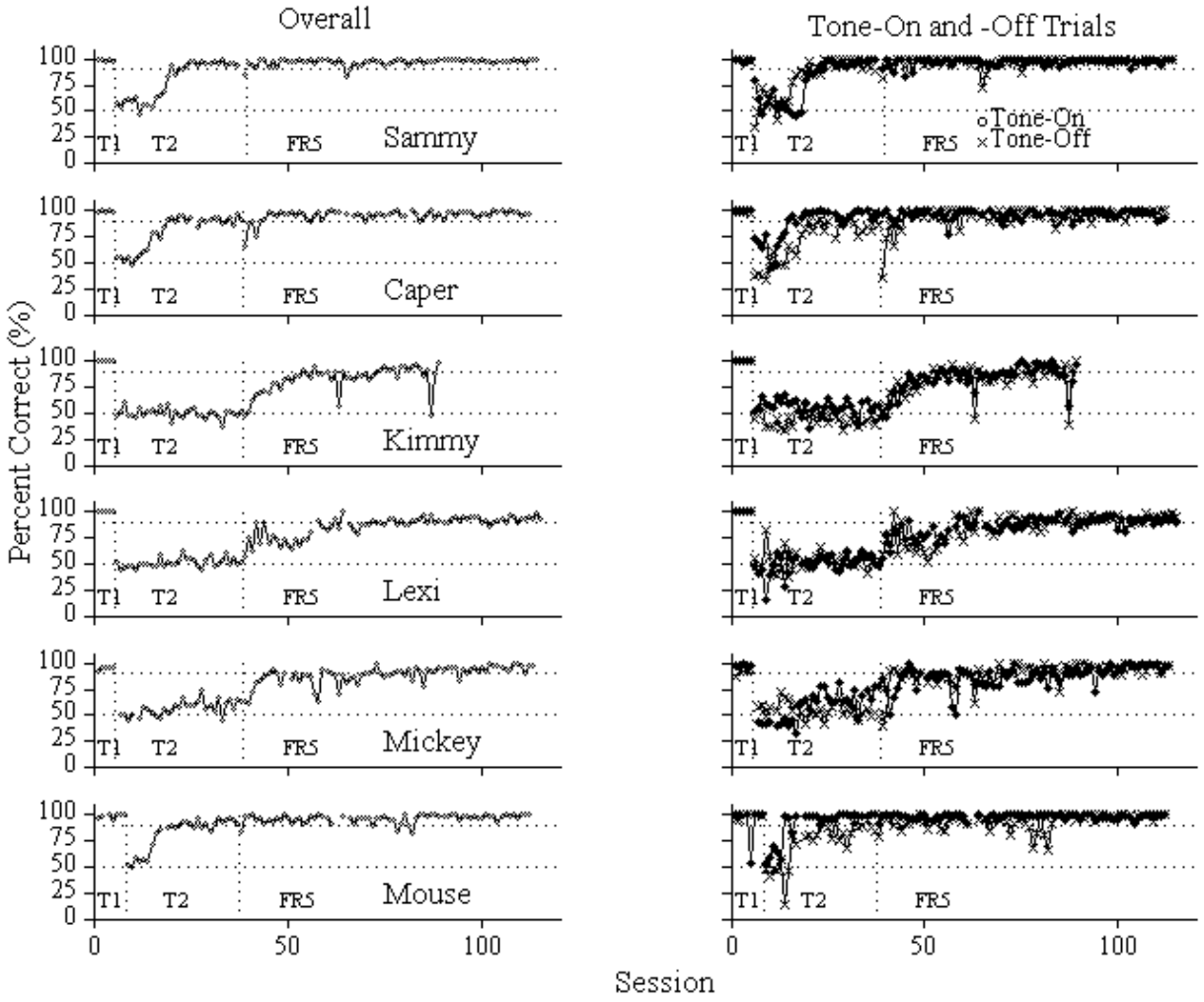

Figure 7. The overall percentages correct (left panel) and percentages correct on tone-on (unfilled circles) and tone-off (crosses) trials (right panel) across sessions during the side lever training with prompts (T1) and the side lever training without prompts (T2) and when the FR 5 was introduced on the central lever during T2 (FR 5).

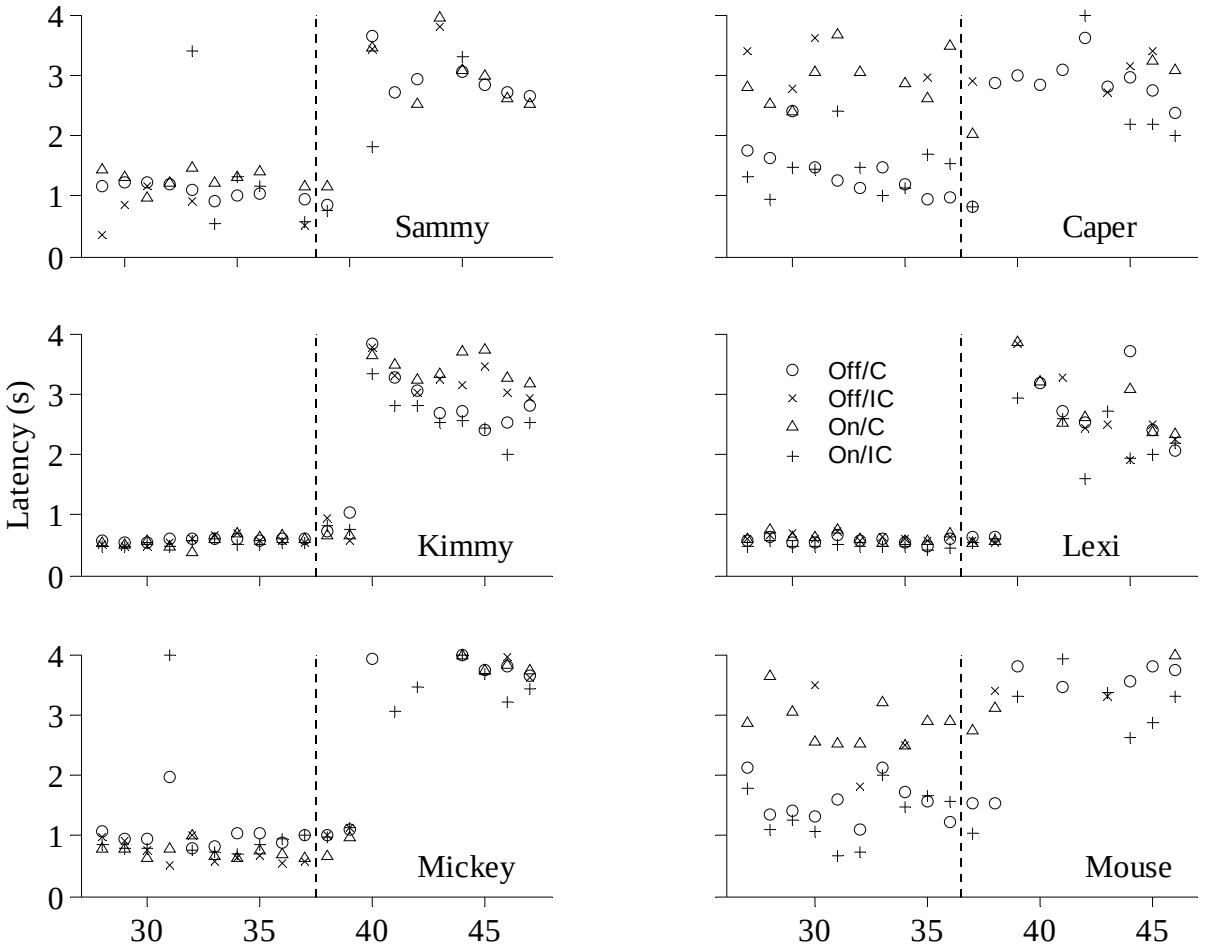

Figure 8. Latencies to correct (On/C) and incorrect (On/IC) responding during trials and to correct (Off/C) and incorrect (Off/IC) responding on tone-off trials plotted against session numbers. The vertical line indicates when the FR 5 was introduced on the central lever during the side-lever training without prompts.

side lever response by the total number of the responses. Figure 8 (on the left side of the vertical line) shows that Sammy, Caper and Mouse (whose response accuracy increased during the T2) had longer latencies to response to the side levers than Kimmy, Lexi and Mickey (whose response accuracy did not increased during the T2). In other words, the duration for which the stimuli (tone and no-tone) were presented for Kimmy, Lexi and Mickey was shorter than for Sammy, Caper and Mouse. To increase the duration of the stimulus presentation for all possums, a Fixed Ratio (FR 5) schedule was introduced on the central lever. Figure 8 (on the right side of the vertical line) shows the latencies of all response types increased for all possums after the second sessions following the introduction of the FR 5. Figure 7 also shows the response accuracy for all trial types increased and eventually reached over 90%. Thereafter, the FR 5 was scheduled on the central lever in the experimental and training conditions except in the lever pressing training for new possums which replaced the deceased possums.

Figure 9 shows the overall percentages correct over all training session for each possum at different tone frequencies plotted against session numbers. The initial training is excluded here. Gaps between data are sessions where the possums did not respond at all or where equipment problems occurred. Horizontal lines mark 90% correct. Vertical lines separate the conditions with different tone frequencies. Each frequency is indicated above each condition. The data presented in Figure 9 for Mickey and Mouse in the 30 kHz conditions are the first 30 and 39 training sessions respectively, which the first probe followed without reaching the training criterion (see more details in Appendix C). For the same

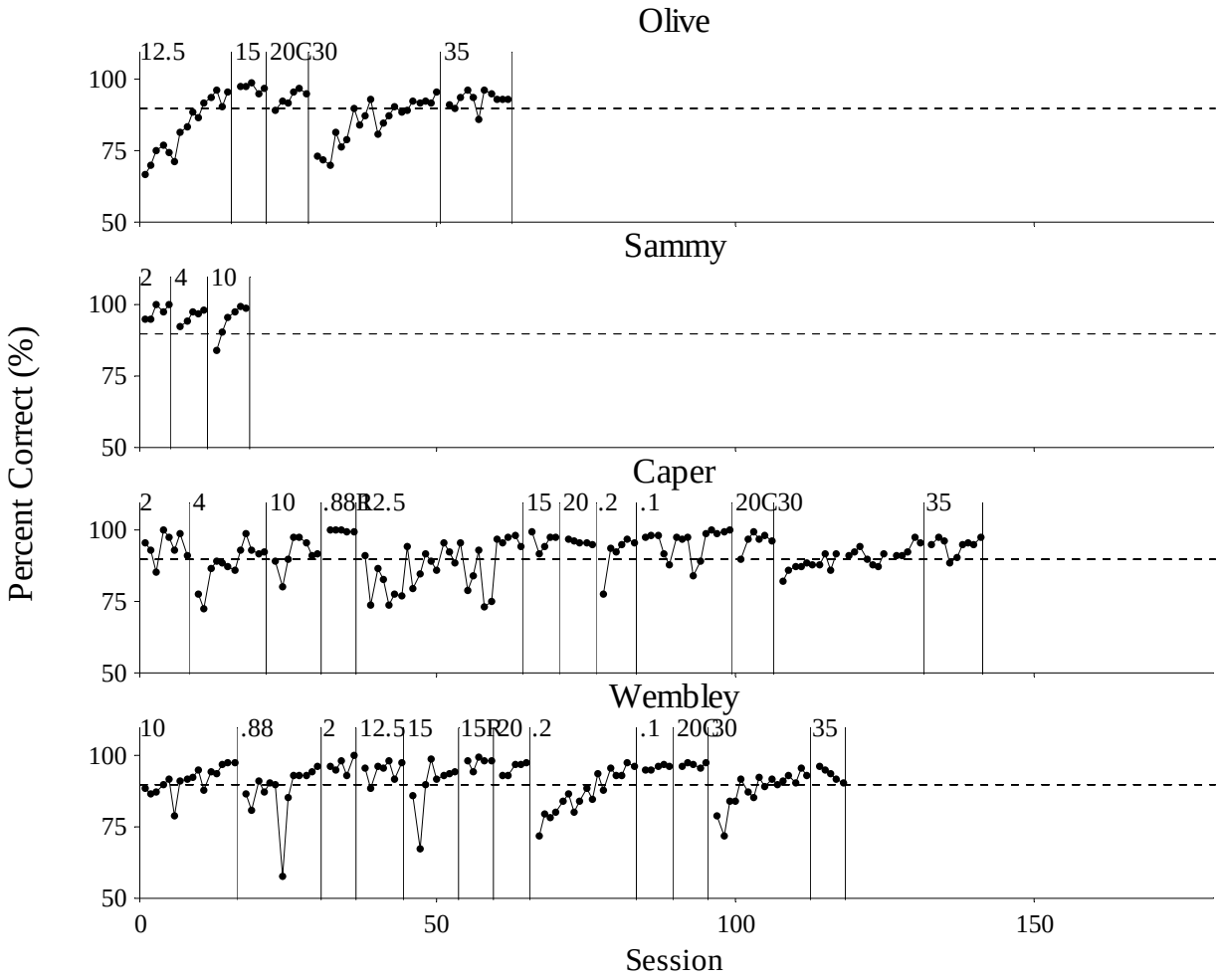

Figure 9. The overall percentages correct plotted against the number of sessions each possum took to complete the initial training in each experimental condition at each frequency (kHz), excluding data from the training condition at the initial frequency. The *R* indicates a repeated condition, and *C* is the condition in which the tone intensity was set using calibrating procedure.

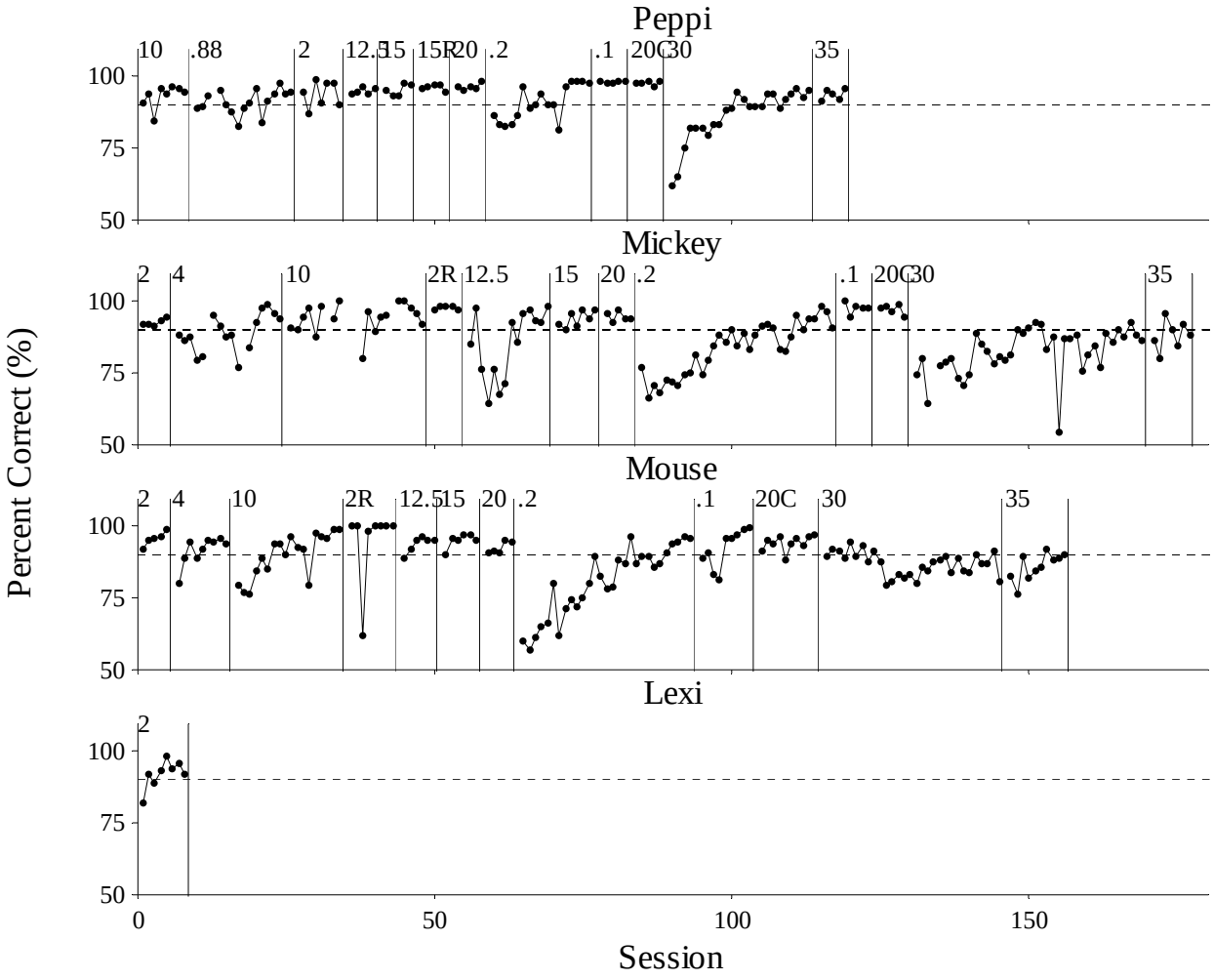

Figure 9 cont.

possums in the 35 kHz condition, the training criterion was changed to reaching an 85% or more response accuracy for five consecutive sessions, and these data are presented here (see more detail in Appendix C).

Figure 9 shows generally the response accuracy is the lowest at the first session in most conditions, and it increased across sessions until reaching the training criteria. Figure 9 also shows all possums required most training sessions in the 30 kHz condition. All possums, except for Caper, required many training sessions after the frequency decreased from 20 to .2 kHz. However, the possums did not required as many training sessions after the tone frequency increased from .1 to 20 kHz.

Experimental Condition

Table 3 presents a numbers of successful probe sessions that each possum completed in a condition at each frequency (kHz). Kimmy was excluded from Table 3, as he did not complete any probes. Table 3 shows each possum completed different numbers of successful probe sessions in different experimental condition. One reason for this was that early in the study all possums stayed in an experimental condition and continued to be probed until they all had completed five probes. The other reason was due to procedural errors being made. All probe data are presented in Appendix D.

Initially, data for each probe session was analysed using each measure (e.g., percentage correct, log *d* and ROC plots). However, there was no consistent difference between the data across all probes for each possum for each measure. Therefore the average performance for each possum was calculated using each

Table 3.

The number of successful probe sessions each possums completed in each condition at each frequency.

Tone Intensity (kHz)	Possums							
	Sammy	Olive	Caper	Wembley	Peppi	Lexi	Mickey	Mouse
.1	-	-	5	5	5	-	5	6
.2	-	-	5	5	5	-	5	5
.88	7	-	5 (5*)	5	5	4	5	6
2	5	5	5	5	5	1	5 (5*)	6 (4*)
4	6	-	6	5	5	-	5	6
10	7	-	5	5	5	-	5	5
12.5	5	5	5	5	5	-	7	5
15	-	5	5	5 (5*)	5	-	6	5
20	-	(6*)	5	5 (5*)	5(6*)	-	5 (5*)	5 (5*)
30	-	6	6	9	7	-	5	6
35	-	5	6	7	5	-	5	5

Note. Asterisks (in bracket) indicate a number of probes in the replicated condition. Dashes indicate no probe session was conducted.

measure and is presented in this section. The average data that were calculated from fewer than three data points were not presented here. Data were also not presented for blocks of trials that reduced tone intensity in tone-on trials to 0 dB(A).

Experimental Conditions

Replicated Conditions

Figure 10 presents the average percentages correct for the probe session for both the first exposure (unfilled circles) and the second (asterisks) exposure to 880, 2000 and 15000 Hz for Sammy, Caper, Mickey, Mouse, Wembley and Peppi, plotted as a function of tone intensity dB(A). A linear regression is the best fitted line to these data points. In the 15 kHz conditions, a modified speaker was used for the first exposure and a tweeter was used for the second exposure. The percentages correct were calculated by dividing the total number of correct responses by the total number of trials (20) in a block, and then multiplying by 100. The data presented here are the average of these values. Figure 10 shows that most of the possums performed with slightly higher response accuracy across all tone intensities during the second exposure than the first exposure.

Figure 11 presents the average percentages correct for all probes for Caper, Wembley, Peppi, Mickey and Mouse and the average across all possums in the 20 kHz (unfilled circles) and the 20 kHzC (asterisks) condition, plotted as a function of tone intensity. Lines on each graph are the best fitted line to the data in each condition. The horizontal lines mark at 50 and 75% correct. Figure 11 shows, except for Mickey, all possums had higher percentages correct across all tone

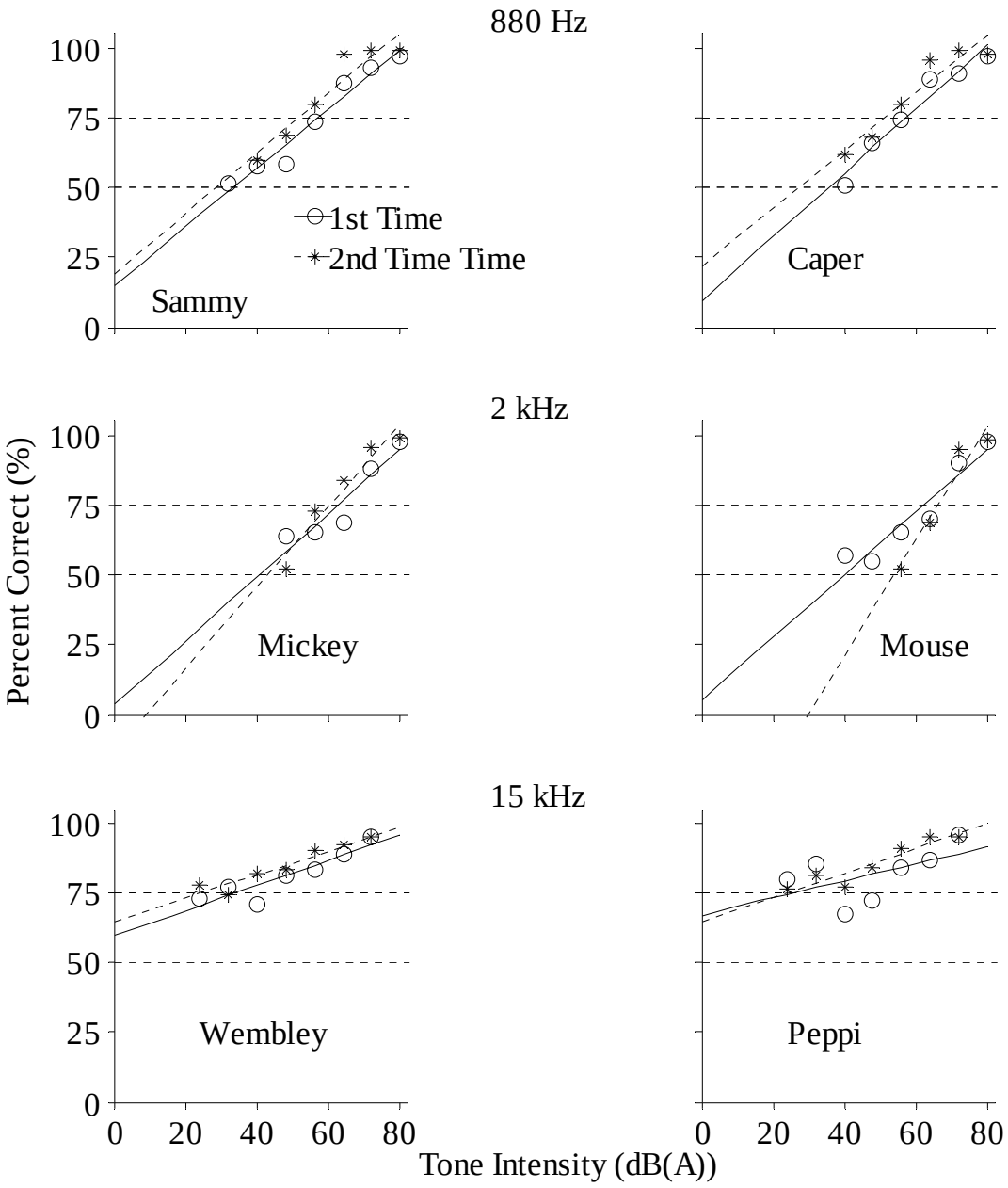

Figure 10. The average percentages correct for the first and the second exposure to a condition at each tone frequency for each possum.

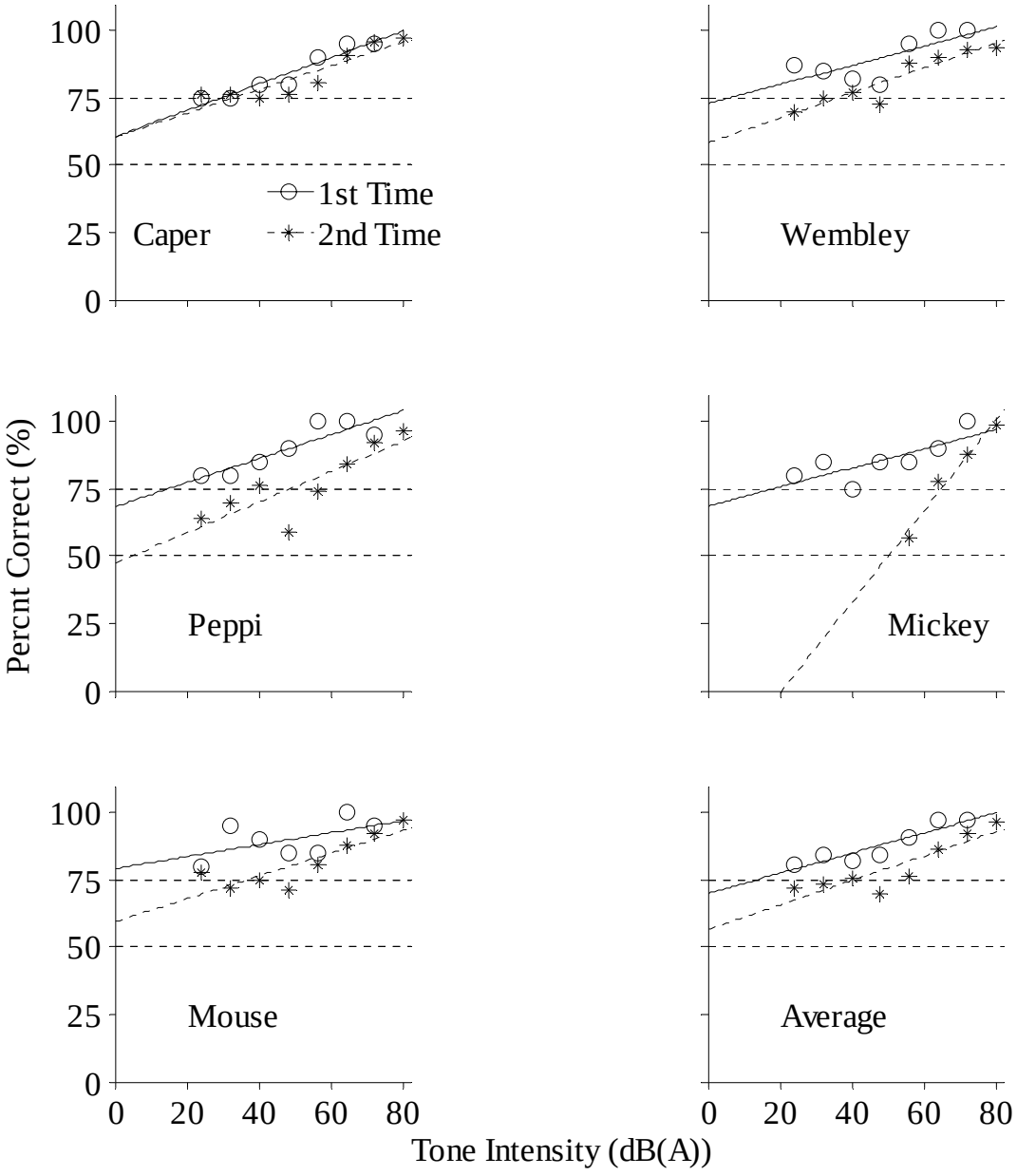

Figure 11. The performance of each possum during probe sessions in both the first and the second exposure to the 20 kHz Condition.

intensities during the first exposure compared with the second exposure, although these differences were small. Thus in the remaining data analysis, the data from the first exposure will be used, but data from both exposures will be presented in the audiogram.

Average Overall Percentages Correct for Probe Sessions

Figure 12 presents, for each possum, the average percentages correct over all probes at each frequency, plotted against tone intensity (dB(A)). The horizontal lines mark 50% and 75% correct. The linear regression line on each graph is presented because this fits best between the data points. Figure 12 shows that for all tone frequencies, the possums discriminated the stimulus well at the high tone intensity (around at the highest and second highest dB(A) values), and their performances generally deteriorated as the volume reduced. The slope is least steep with the high frequency tones, between 12.5 and 30 kHz for Caper, Peppi and Mouse, and between 15 and 35 kHz for Wembley and Peppi, and Mickey with the exception at 20 kHz. This indicates the possums detected the tone well.

Average Percentages Correct for Tone-On and –Off Trials in Probes

Figure 13 presents the average percentages correct during tone-on (unfilled circles) and tone-off trials (filled circles) for each possum plotted against the tone intensity (dB(A)). The horizontal lines are at 50% and 75%, respectively. The percentages correct for a trial type (i.e., tone-on or tone-off) were calculated by dividing the total number of correct responses in this trial type by the total number of trials in the trial type, and multiplied by 100. The averages of these values for each possum in each condition are presented.

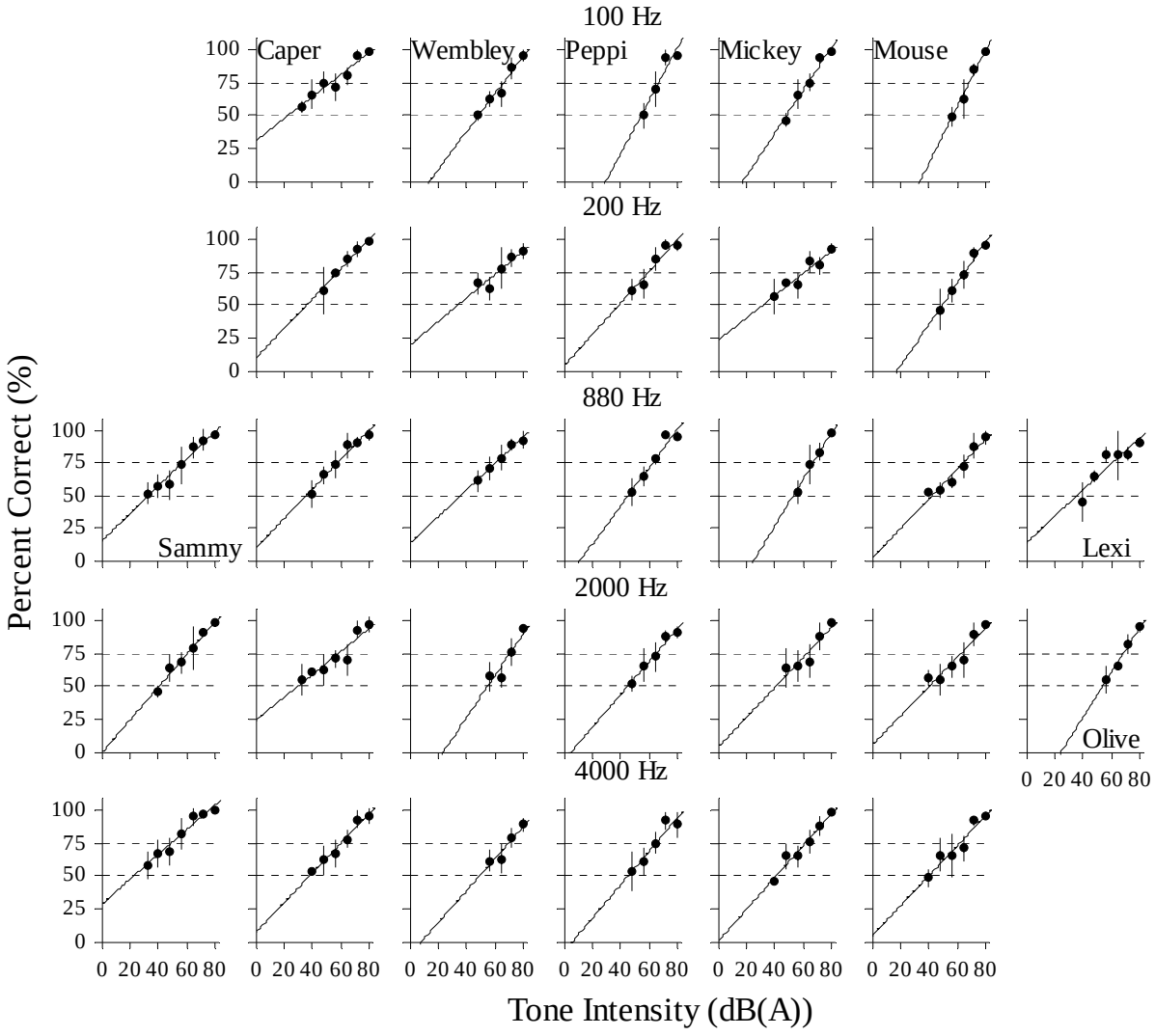

Figure 12. The average percentages correct for each possums in experimental conditions at100, 200, 880, 2000 and 4000 Hz, plotted as a function of tone intensity (dB(A)).

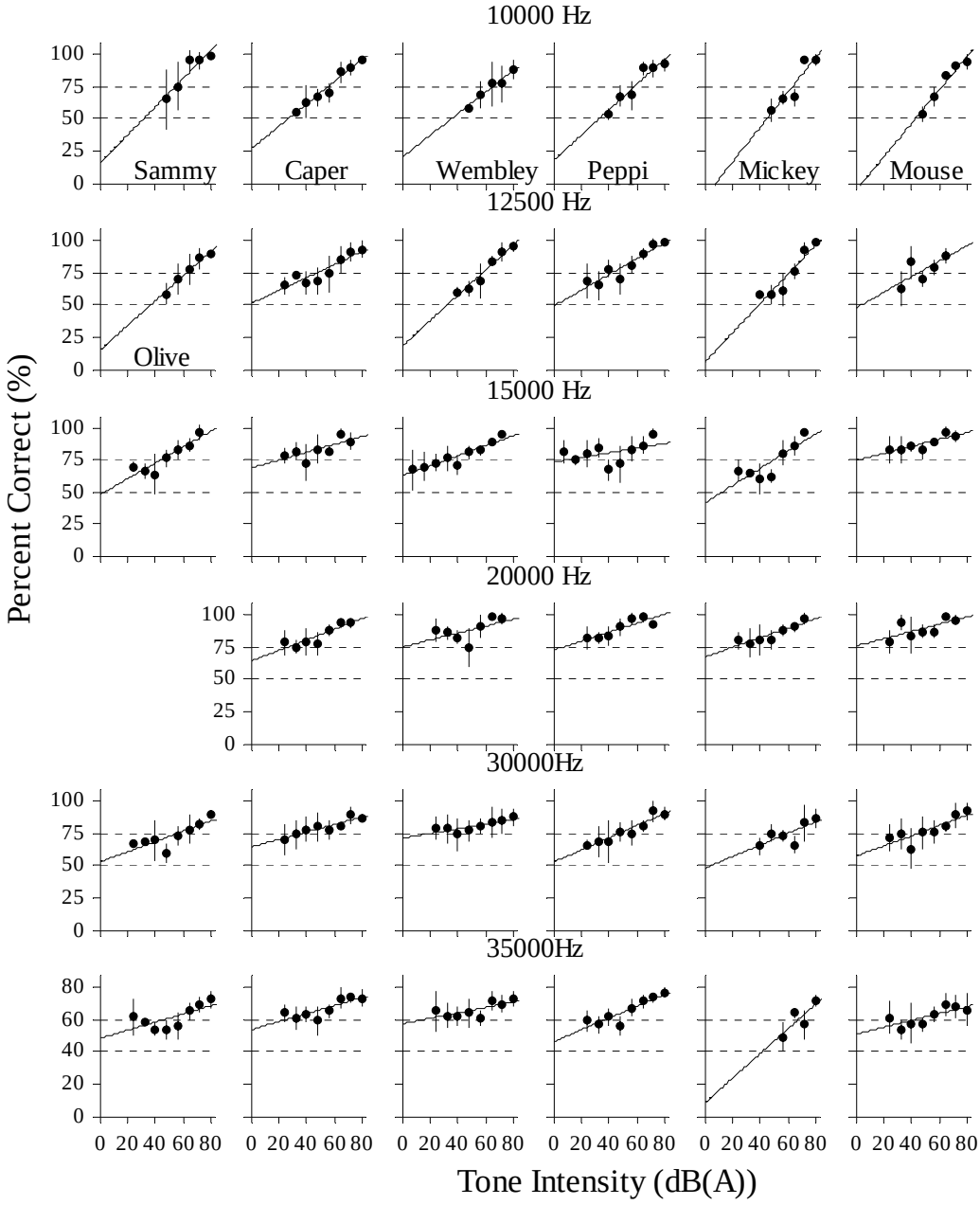

Figure12 cont. The average percentages correct for each possums in experimental conditions at10, 12.5, 15, 20, 30 and 35 kHz, plotted as a function of tone intensity (dB(A)).

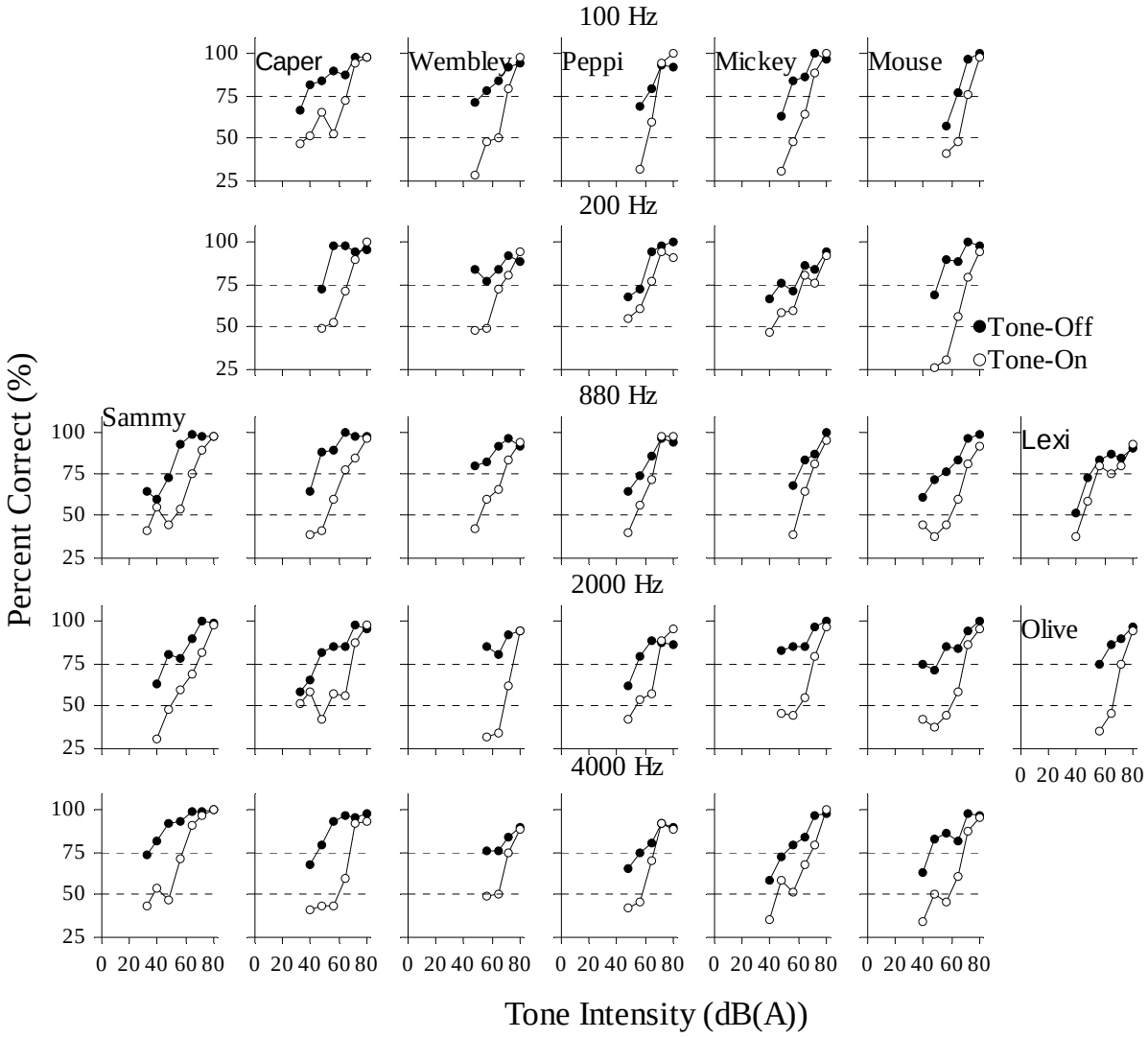

Figure 13. The average percentages correct for tone-on and tone-off trials, separately for each possums in experimental conditions at100, 200, 880, 2000 and 4000 Hz, plotted as a function of tone intensity (dB(A)).

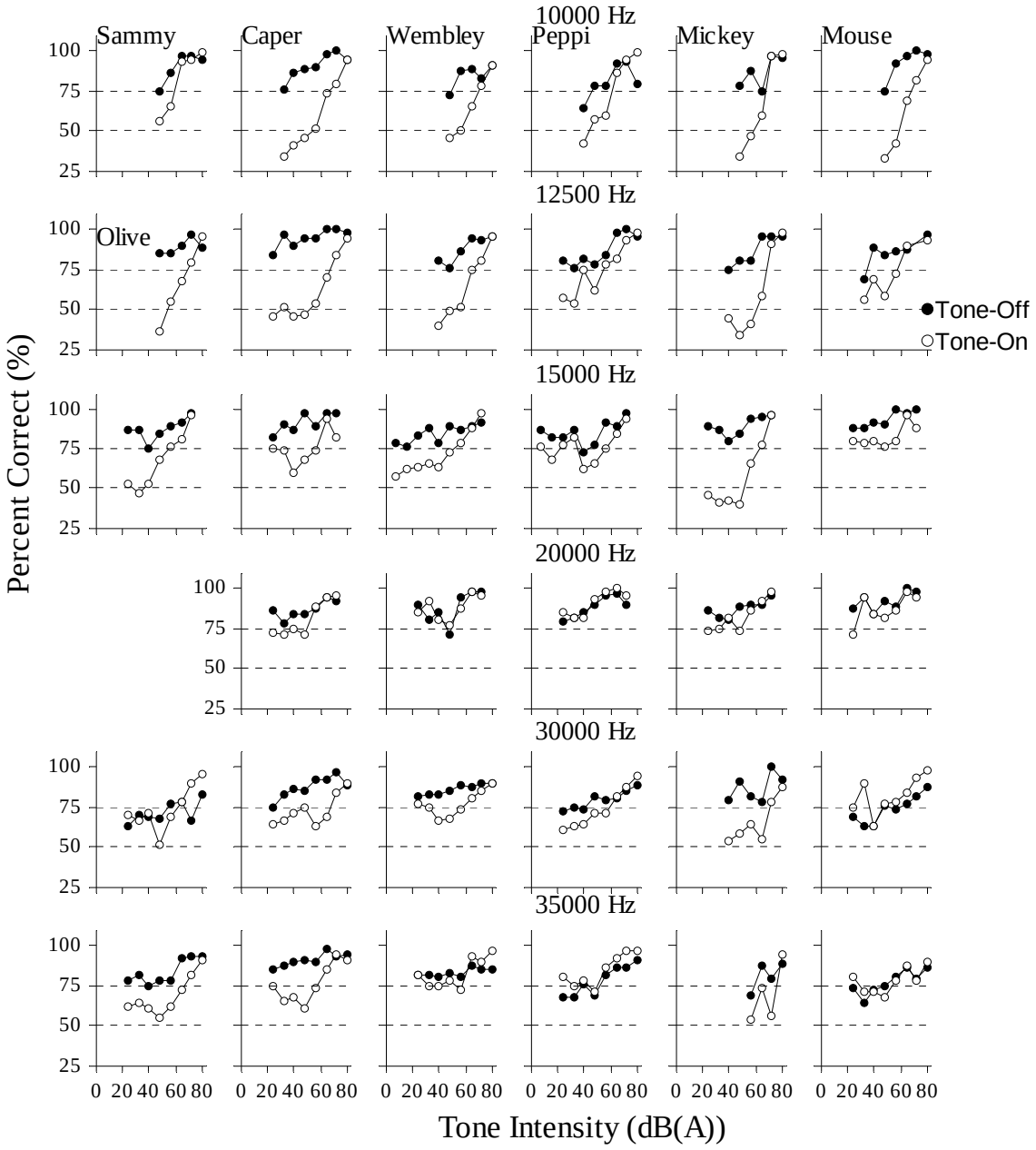

Figure 13 cont. The average percentages correct for tone-on and tone-off trials, separately for each possums in experimental conditions at10, 12.5, 15, 20, 30 and 35 kHz, plotted as a function of tone intensity (dB(A)).

Figure 13 shows, for all possums the response accuracies for tone-off trials were generally greater than for the tone-on trials at most tone intensity. The response accuracies for tone-on trials decreased more steeply than those for tone-off trials, as the tone intensity reduced. This difference became more apparent as the tone intensity reduced, and also in lower frequency conditions. In both of these cases, the average percentages correct are also generally low (also see Figure 12).

Average Log d for Probes

Each log *d* value for correct responses in each block was calculated by using Equation (4). A problem arose when an indefinite log *d* value resulted. This occurred when the possum demonstrated a perfect discrimination in a block. Davison and Nevin (1999) suggested that the most appropriate way to solve this problem in this type of data is to use a log-linear rule that suggested by Hautus (1995). In the log-linear rule or also called the Hautus correction, a value of 0.5 was added to all response types (Hautus, 1995). In the current study, this value was added to all response type, hits, correct rejections, misses and false alarms that were recorded in each block. For example, if the number of hits was 10, the number of correct rejections was 10, the number of misses was 0, and the number of false alarms was 0, to calculate the log *d* value, a value of 10.5 for the hits and the correct rejections, and a value of 0.5 for misses and the false alarms were used.

Figure 14 presents the average log *d* values for each possum, plotted as a function of tone intensity for each frequency. The horizontal lines mark at 0 and 0.48. A best fitted linear regression is drawn each data set. All data are similar to that from the average percentages correct analysis (Figure 12). All possums

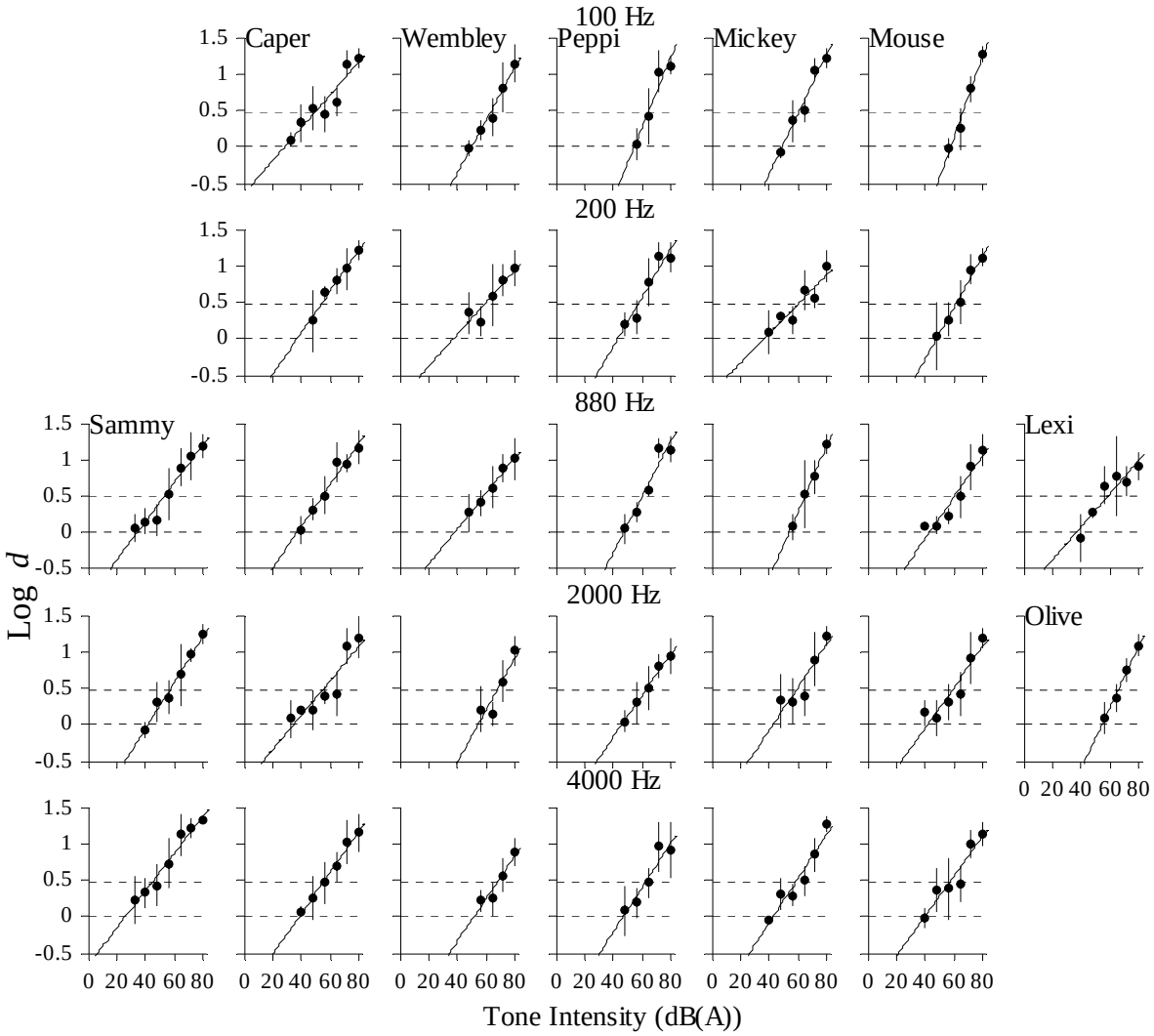

Figure 14. Average log *d* in experimental condition with the 100, 200, 880, 2000 and 4000 Hz tone for each possums plotted as against each tone intensity (dB(A)).

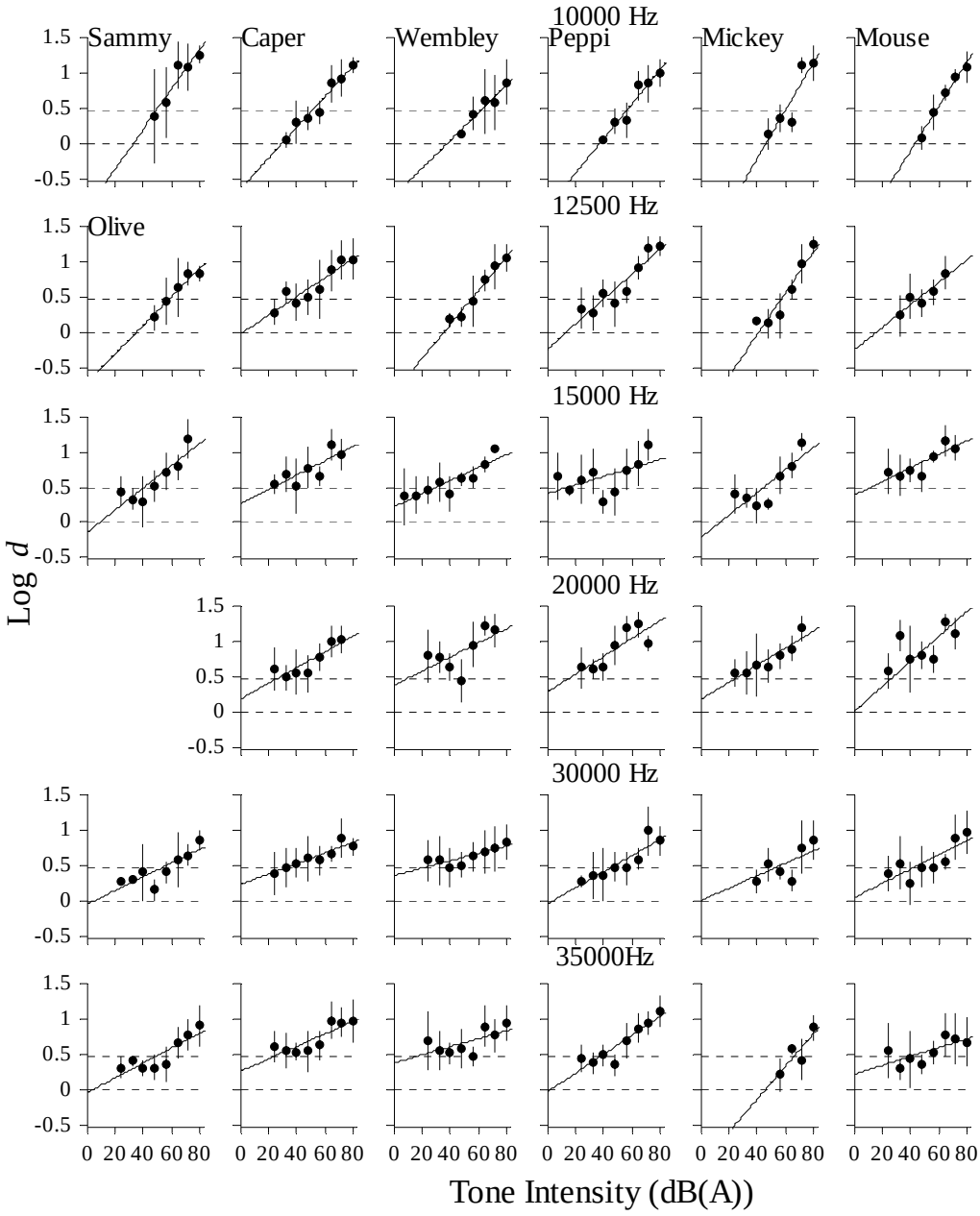

Figure 14 cont. Average log *d* in experimental condition at 10, 12.5, 15, 20, 30 and 35 kHz for each possum plotted against each tone intensity (dB(A)).

perform well at the high dB(A) values and this deteriorates as the volume reduces. With the high frequency tone, the slopes are generally less steep for all possums.

Log c

Average log *c* values for each possum in each frequency condition are plotted against the tone intensities dB(A) and are presented in Figure 15. Horizontal lines mark zero. Each log *c* value was calculated by using Equation (3) and the Hautus correction, and the averages of these are presented in Figure 15. In Figure 15, most of the data points fall below zero, and in many cases the log *c* values, at the highest and the lowest tone intensities, are generally close to or above zero. In many cases log *c* values are also closer to zero at these higher tone frequencies. The exceptions are Peppi at 20 and 35 kHz, and Mouse at 30 kHz, where it is shown that most data points are above zero. In addition, for Mouse at 35 kHz, most of the data points are on zero. For most possums, the data points fell below zero indicating the possums had a bias towards the 'no' or left manipulandum, and the bias decreased or shifted towards the right manipulandum at the higher tone frequencies. In many cases the lowest bias occurred at the highest and lowest tone intensity values. For two possums (Peppi and Mouse) the data points are above zero indicating the bias towards the 'yes' or right manipulandum. For Mouse, at 35 kHz, the data points were on zero indicating there was no apparent bias towards any of the levers.

ROC analysis

Figure 16 shows average ROC analyses for each tone frequency for each possum, presented with the proportion of hits (correct responses in the tone-on

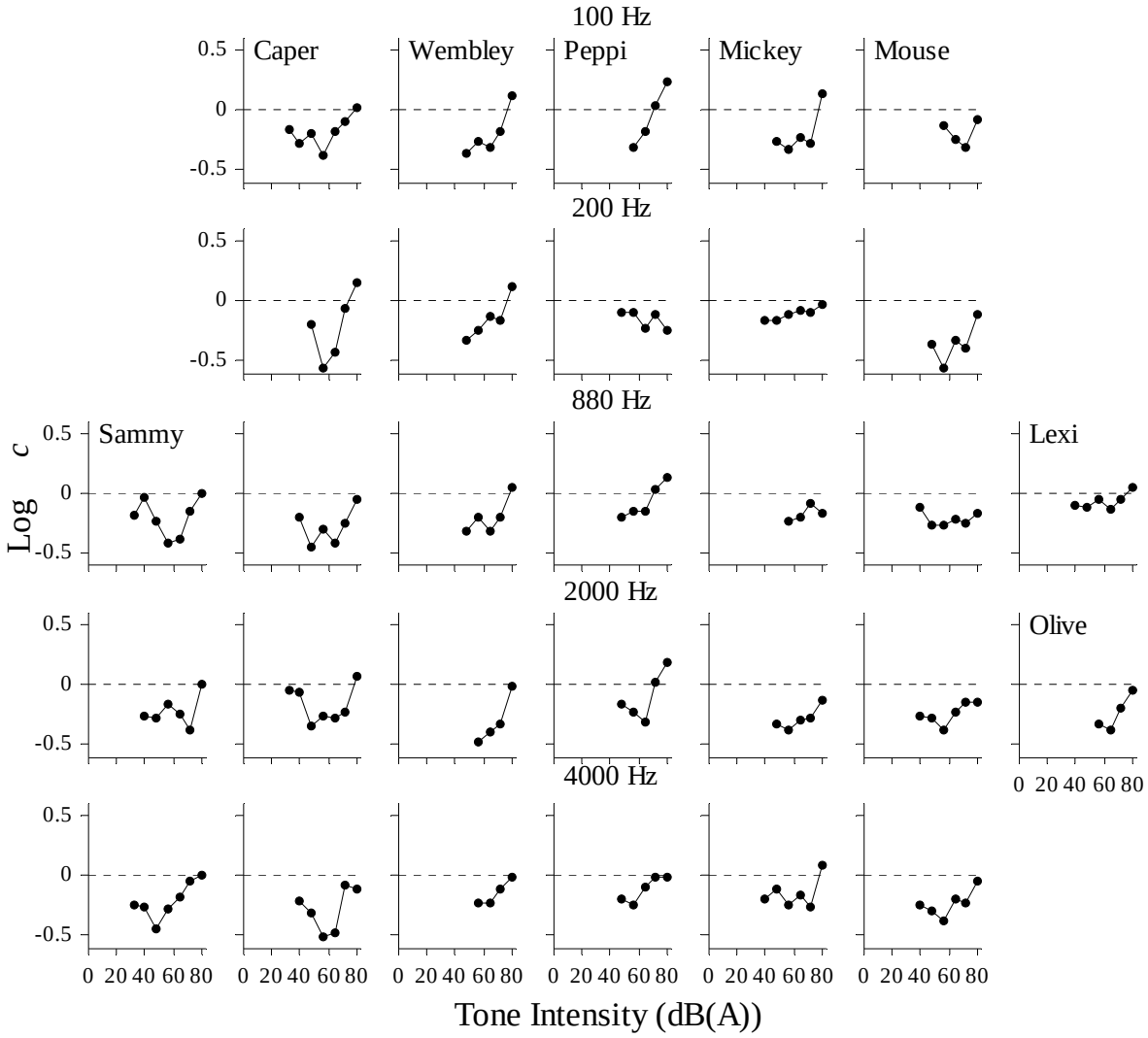

Figure 15. Average log *c* for 100, 200, 880, 2000 and 4000 Hz conditions for each possum plotted as a function of tone intensity (dB(A)).

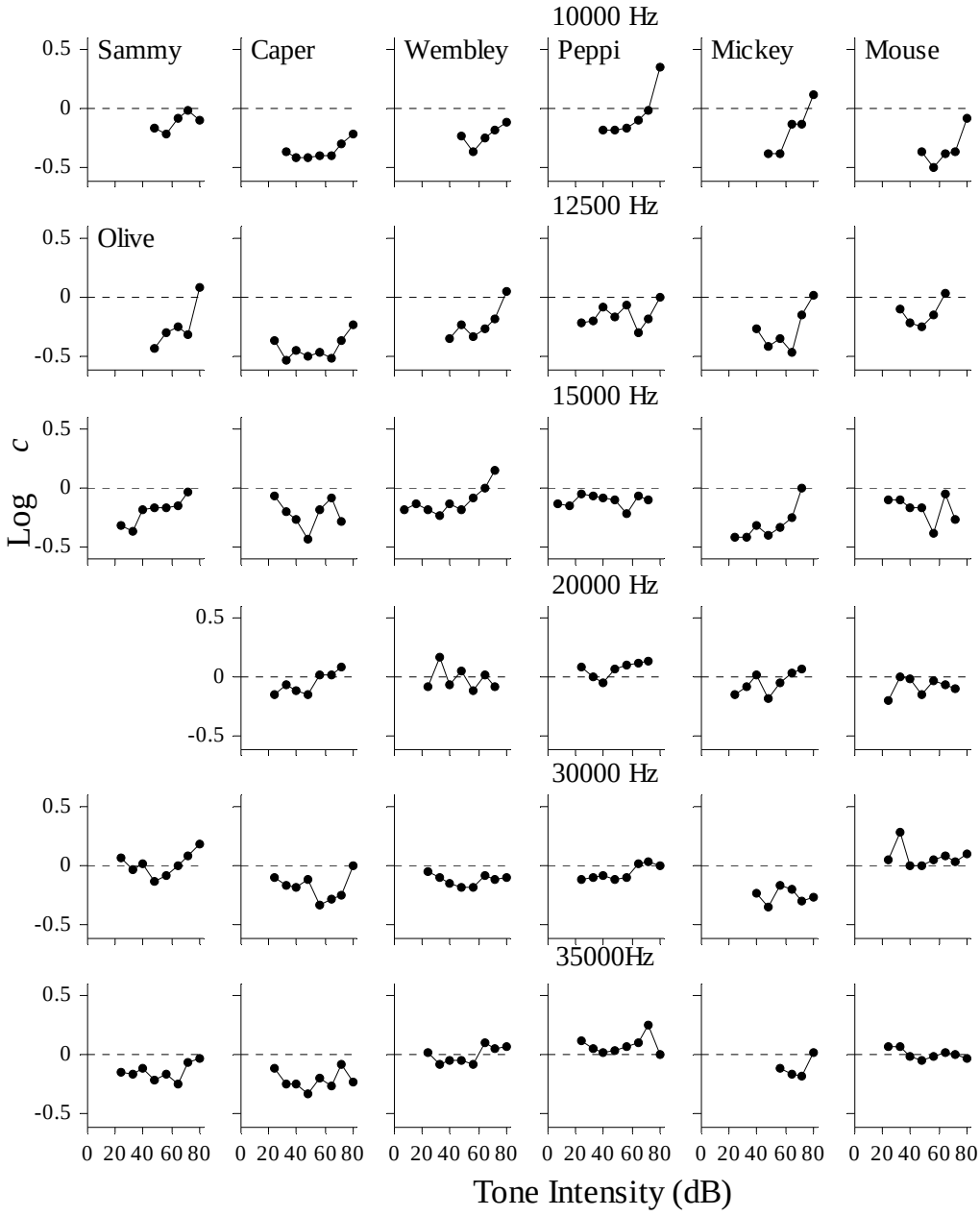

Figure 15 cont. Average log *c* for 10, 12.5, 15, 20, 30 and 35 kHz condition for each possum plotted as a function of tone intensity (dB(A)).

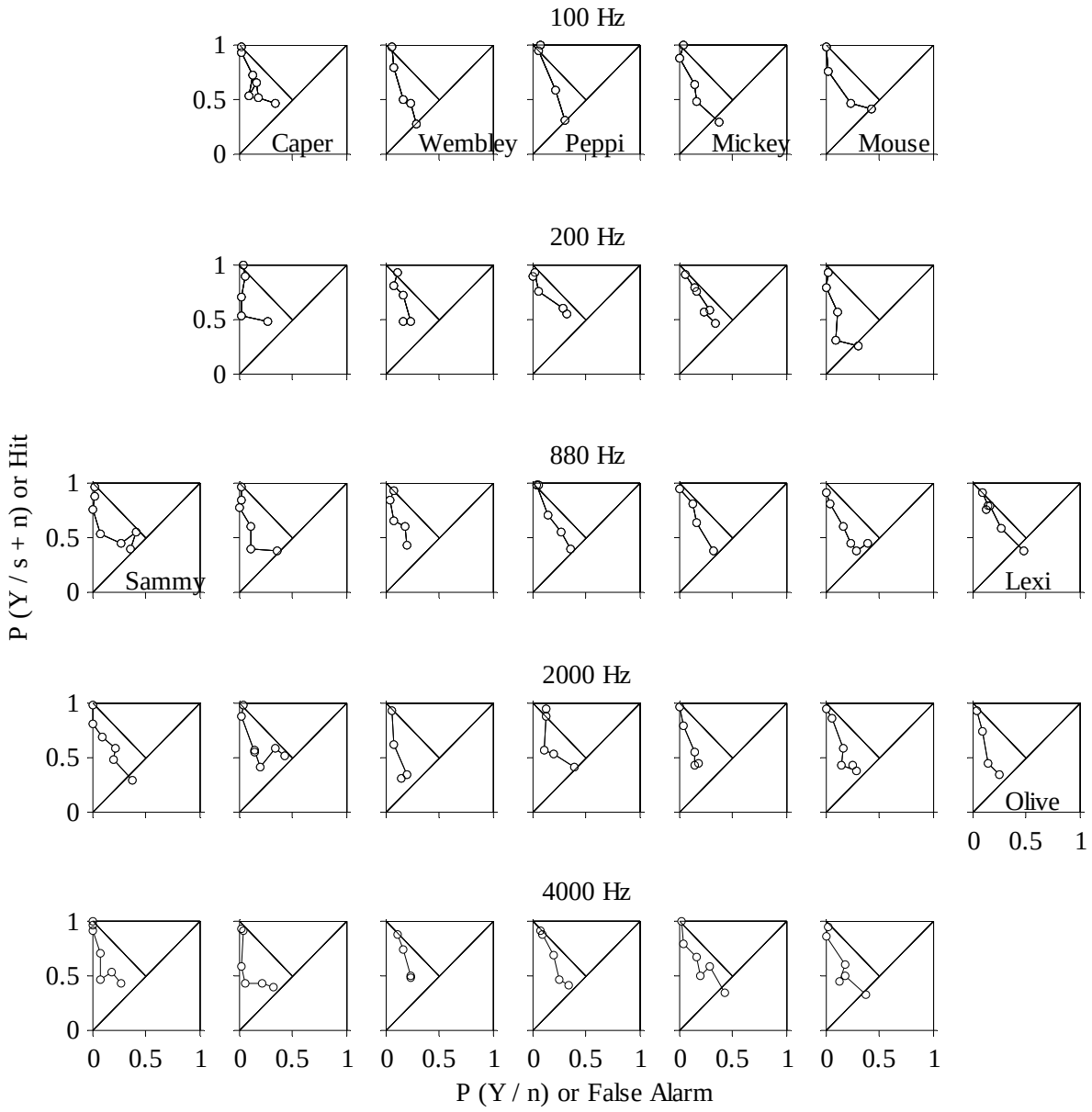

Figure 16. Average ROC plots for each condition with the 100, 200, 880, 2000 and 4000 Hz tone for each possum.

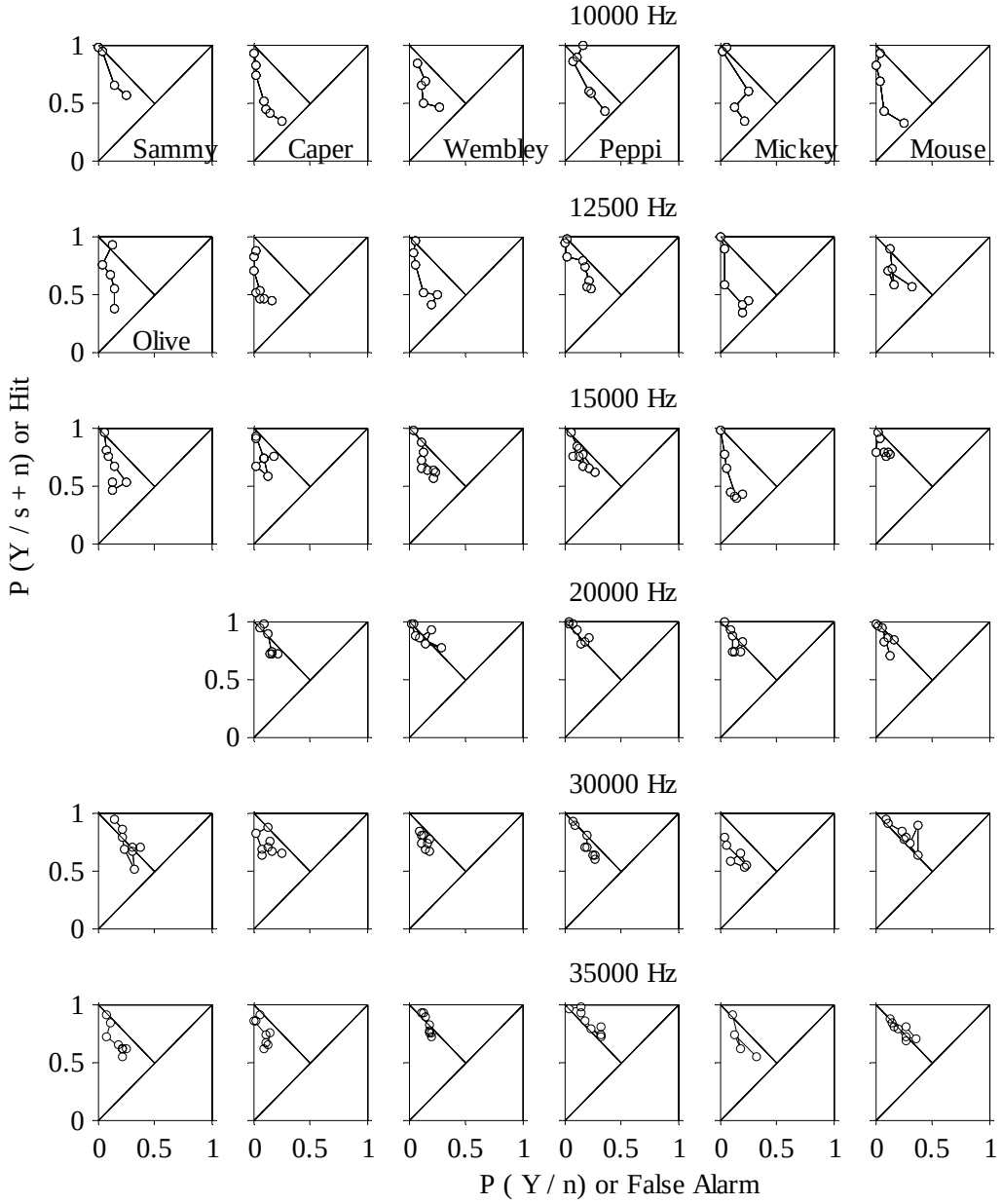

Figure 16 cont. Average ROC plots for each condition with the 10, 12.5, 15, 20, 30 and 35 kHz tone for each possum.

trials) plotted against the proportion of false alarms (incorrect responses in the tone-off trials). All data points are joined in the order of the block presentation. Figure 16 shows in most cases the first plot fell on the left top corner, this indicates that the possums responded with high accuracy during tone-on trials in the first block with the highest tone intensity. For most cases, the data points fell to the left side of the minor diagonal ranging from the left top corner towards the major diagonal. This indicates that the possums tended to respond on the 'no' manipulandum during tone-on trials (or had numbers of misses), and as tone intensity reduced, the response accuracy decreased. In many cases, the distance between the data points and the minor diagonal increased, and in some cases, this distance reduced at the end, this indicates that the left lever bias increased as the tone intensity reduced and the a small bias occurred at the low tone intensity. For Peppi at 20 and 35 kHz, and for Mouse at 30 kHz, the data points are generally on the right side of the minor diagonal and for Mouse at 35 kHz, most of the plots are on the minor diagonal. In the cases the data points are the right side of the minor diagonal line indicating the possum responded more on the 'no' manipulandum during the tone-on trials. In the cases the data points are on the minor diagonal indicating the possums responded with the equal proportion on the 'yes' and 'no' manipulandum during the tone-on trials. Generally at the tone frequency between 12.5 and 35 kHz, most data points are near the left top corner and also very close to or on the minor diagonal, this means that the possums response accuracy did not reduced much as the tone intensity reduced, and they responded in approximately equal proportions to the 'yes' and 'no' manipulanda on tone-on trials.

Two types of threshold values were estimated based on the percentages correct and log *d* analyses. To estimate threshold values (dB(A)), initially the equation of each linear regression in Figure 12 and 15 are calculated. By using this equation, the threshold (tone intensity) values for threshold criterions (i.e., 75% correct for the average percentages correct analysis; and 0.48 for log *d* analysis) are estimated. This value should be the tone intensity which each of the best fitted line crossed at the threshold criterion lines. Threshold values for the repeated 20 kHz condition were also calculated in the same way but based on Figure 11.

Audiograms

The threshold values were calculated which are shown Figures 17 and 18 on the overall percentages correct and log *d* analyses were used to produce an audiogram. Figure 17 presents threshold values for each possum, and the average for all possums, based on the percentages correct analysis for overall trials (Figure 12) and are plotted as a function of tone frequency (kHz). Asterisks present the threshold values for the repeated 20 kHz condition that used the calibrating procedure. Each line on the graph is the best fitted curvilinear regression line for all data points. Figure 17 shows the estimated threshold value for Mouse at 20 kHz was a negative value and could not be plotted but it is indicated on the graph. For all possums, the threshold values for the repeated 20 kHz condition are higher than the first 20 kHz condition. For all possums, high threshold values are found at lower tone frequency. For most possums, these values decreased as tone frequency increased until 15 kHz, where it remained stable between 20 and 30 kHz, and increased slightly at 35 kHz. Mickey's threshold values were generally higher

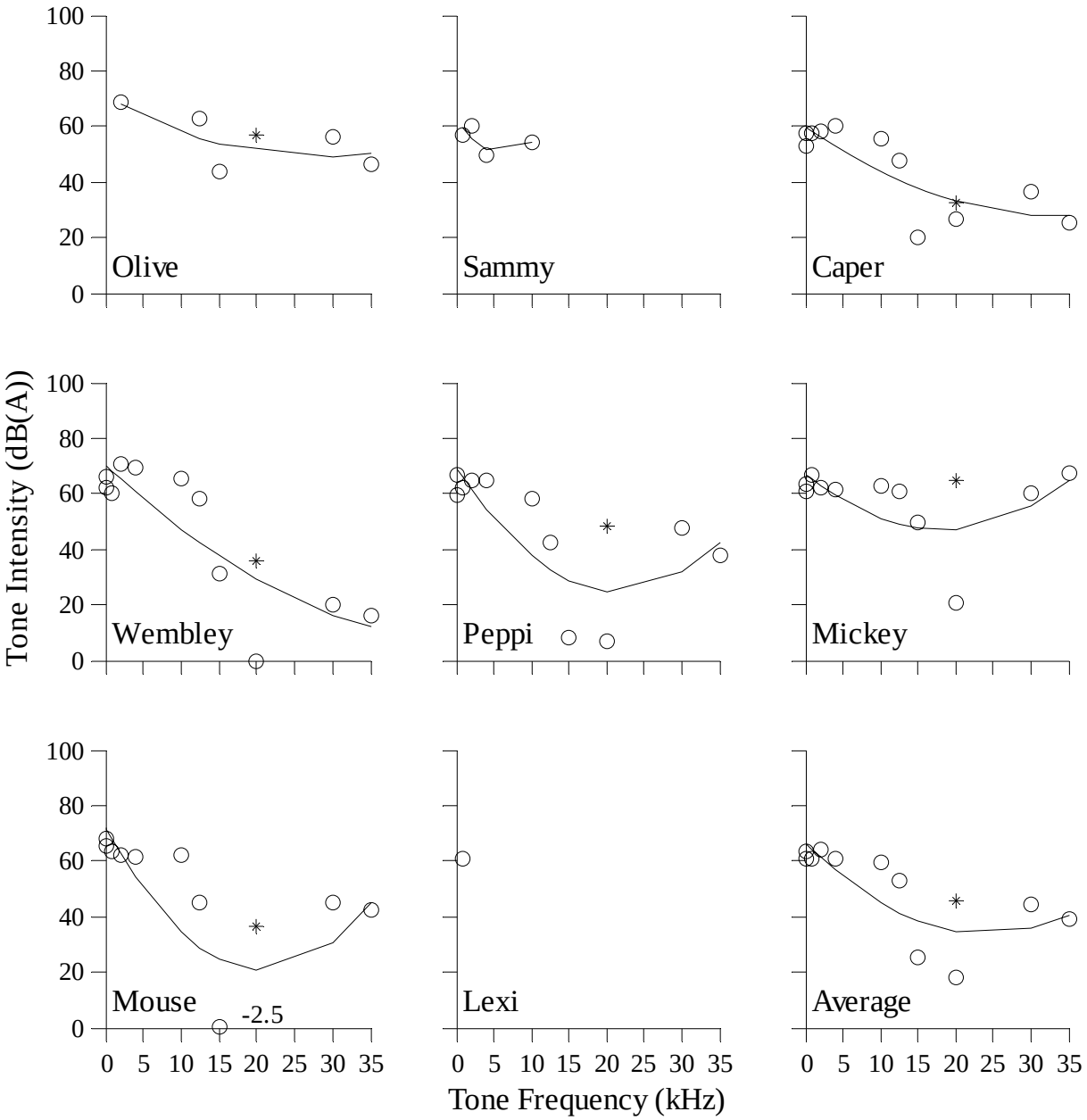

Figure 17. Audiogram drawn based on the overall percentages correct analysis.

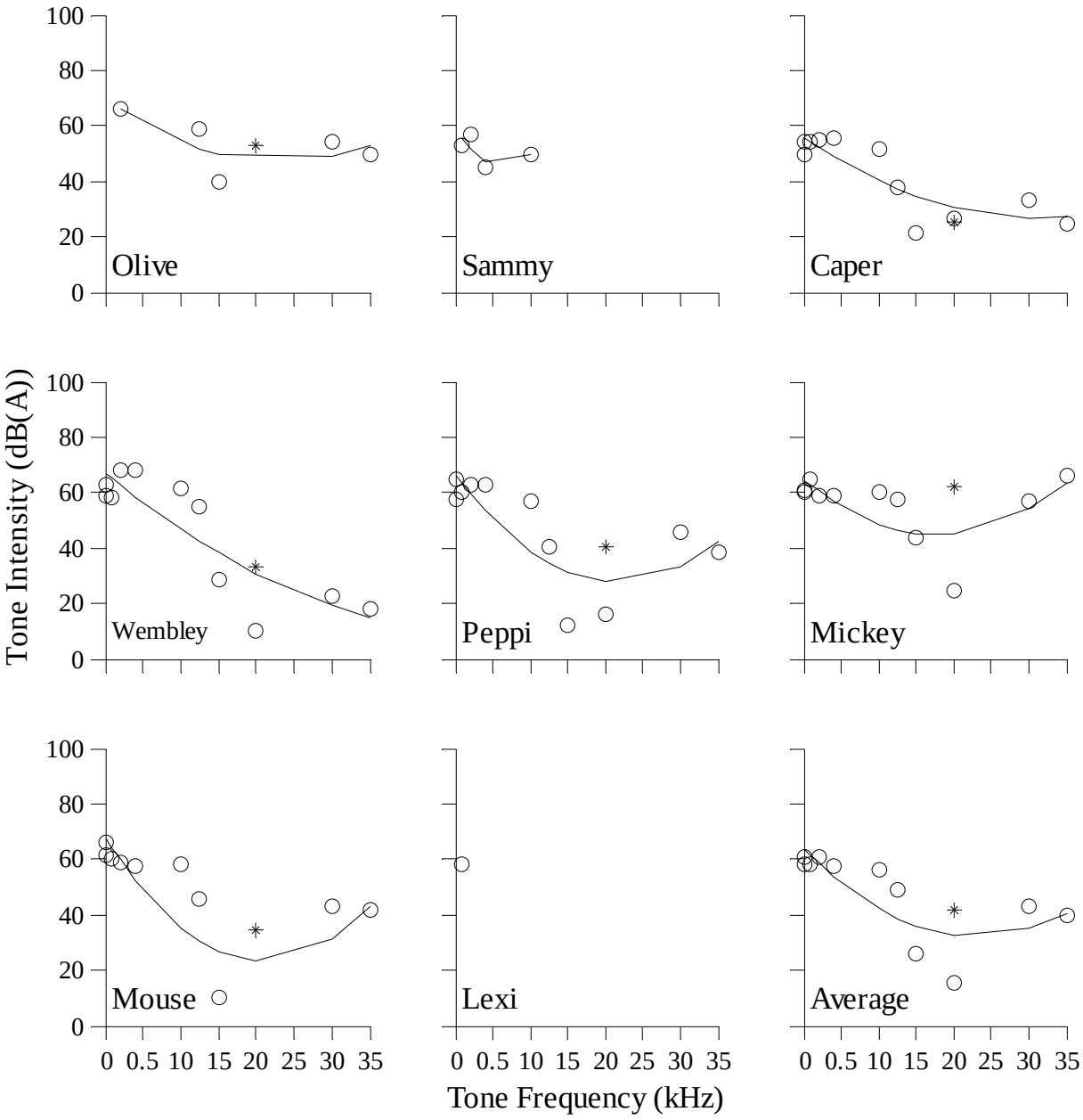

Figure 18. Audiogram drawn based on Log *d* analysis.

across all tone frequencies compare with other possums. Only Wembley showed a monotonic decrease in his threshold values as tone frequency increased. Trends are unable to be discussed for Sammy and Lexi did not have many data points because they died during the experiment although the data are also included in the average data.

Figure 18 shows threshold values for each possum and the average based on the log *d* analysis (Figure 15), plotted as a function of tone frequency (kHz). The line on each graph is the best fitted curvilinear regression line for all data points.

The shape of the function in Figure 18 for each possum, and the average across possums, is similar to that in Figure 17, and shows the same results as for Figure 17.

DISCUSSION

The main aim of the current study was to measure the hearing ability of possums and produce a behaviour-based audiogram. The results from this study indicate that the possums were able to respond at 85 or 90% accuracy to tones between 100 Hz to 35 kHz at 64 to 80 dB(A). Audiograms based on the average percentages correct for overall trials (Figure 17) and log *d* analyses (Figure 18) were produced, and gave quite similar functions. The possums were most sensitive to tones of between 15 to 35 kHz, and were extremely sensitive to tones between 15 and 20 kHz. The audiograms showed the sensitivity of possums increased as the tone frequency increased from 100 Hz up to around 15 kHz, and then it remained stable until 30 kHz, and there was a slight decrease at 35 kHz.

Gates and Aitkin (1982) conducted a microphone mapping survey of the auditory cortex of possums, and found the best hearing frequency was between 330 Hz and 39 kHz with the greatest sensitivity range of between 17 and 19 kHz. Gates and Aitkin (1982) noted that in general, the possums' hearing was most sensitive at around18 kHz. Thus the audiograms based on the behavioural data here and that based on the physiological data are similar.

Ravizza et al. (1969) using conditioned suppression found the best hearing of opossums *(Didelphis virginiana*) was observed between 16 and 32 kHz. The audiogram showed that the opossums' hearing sensitivity increased as the tone frequency increased to around 2 kHz, and remained stable until around 32 kHz and then decreased to 64 kHz. Their results are very similar to that found the current study.

The present study did not test tones as high as 64 kHz. However, given the possums' and the opossums' results over the range studied were similar, the opossums' data could be used to extend the possums' audiogram. Based on the opossums' data, possums might be able to hear the sound at 64 kHz at around 80 dB(A). Ravizza et al. (1969) did not study the lower frequencies with their opossums but they did predict that the opossums should hear the tone between 250 Hz to 70 or 80 kHz. The result from the possums for the current study suggests that this should be the case and the opossums might be able to hear tones as low as 100 Hz.

Aitkin et al. (1979) conducted a cochlear microphonic potentials (CM) study for possums and cats, and found that for both possums and cats the most sensitive hearing range was between 800 Hz and 1 kHz. Their hearing sensitivity increased as the tone frequency increased from 100 to 800 Hz, and then decreased as the tone frequency increased from 1 kHz to 10 kHz, but they did not study any frequencies over 10 kHz. In the current study, the sensitivity for possums continued to increase from 100 Hz to well beyond 10 kHz. Aitkin et al. (1979) noted that testing high frequency tones required further study. The present study also suggested this is needed for the further comparison between the CM and behavioural data.

In terms of the orderly representation of sound frequency in a "cochlear place" in the auditory cortex, macaque monkeys, owl monkeys and grey squirrels are reportedly all similar to possums. However, no audiograms of these species are available for the comparison with the present data.

Winter (1976) reported the frequency of possum calls ranged from 500 Hz to over 12 kHz. However, Winter (1976) was unable to record and measure frequency calls over 12 kHz because of the limitations of his equipment. He reported that it may be possible that possum calls could reach higher frequencies than 12 kHz. Thus, it would be worthwhile investigating the full frequency range of possum calls with equipment that is able to record and measure the high frequencies to compare with the current results.

The current study found that the shapes of the functions shown in the audiograms were slightly different across possums**.** For example, Mickey's sensitivity to tones was relatively poor across all tone frequencies, particularly the higher frequency tones compare with other possums, while Caper and Wembley's overall sensitivity to tones was relatively high across all tone frequencies, particularly at higher frequencies compare with other possums.

One possible reason for this difference may due to the age of possums. As was shown in Table 1, Mickey was 8.5 years of age and Caper and Wembley were between 1 and 1.5 years. The possums' life span in the wild is over 10 years (Cowan, 1990), and in the laboratory where this study was conducted, the possums live up to around 12 to13 years. Therefore Mickey could be considered as old, while Caper and Wembley could be considered as young. If hearing sensitivity in possums are comparable with human, it is possible that the sensitivity of possums hearing reduces with age as has been found for humans (e.g., Brant & Tozard, 1990), especially with high frequency tones (Human Hearing, 2008). Thus age might contribute to the difference in the threshold values for possums. However, there was

only one old possum, and also another young possum, Peppi, had a mixed result from Caper and Wembley. Peppi had generally high hearing sensitivity across all tone frequencies, but his hearing sensitivity at the higher tone frequencies was not as sensitive as Caper and Wembley's. Therefore it will require more research before concluding the relationship between the age of possums and their hearing sensitivity.

Comparison with Signal (2002)

An aim of the current experiment was to compare the results from the 880 Hz condition in this study with those from Signal's (2002) study. It must be noted that there were two procedural differences between the study by Signal and the current study. One was the different number of successful probe sessions. Signal conducted 10 probe sessions for each possum, whereas in the current study the number of probe sessions for each possum varied from four to seven. Another difference was the cut-off criteria used for Peppi and Wembley in a probe session. For the current study it was 60% correct rather than 50% correct which was used by Signal.

To compare the two studies, all data from successful probes with the 880 Hz tone were analysed using the same procedures as Signal used. Signal averaged the raw data from the probes before calculating the other measures while the data presented in the current study were based on averages of the measures calculated from the raw data. Thus, in comparison with Signal's data, the numbers of each response type (hits, correct rejections, misses and false alarms) for each block of 20 trials in a probe were averaged for each possum. These averages were used to calculate the total percentages correct for overall trials, the total percentages correct

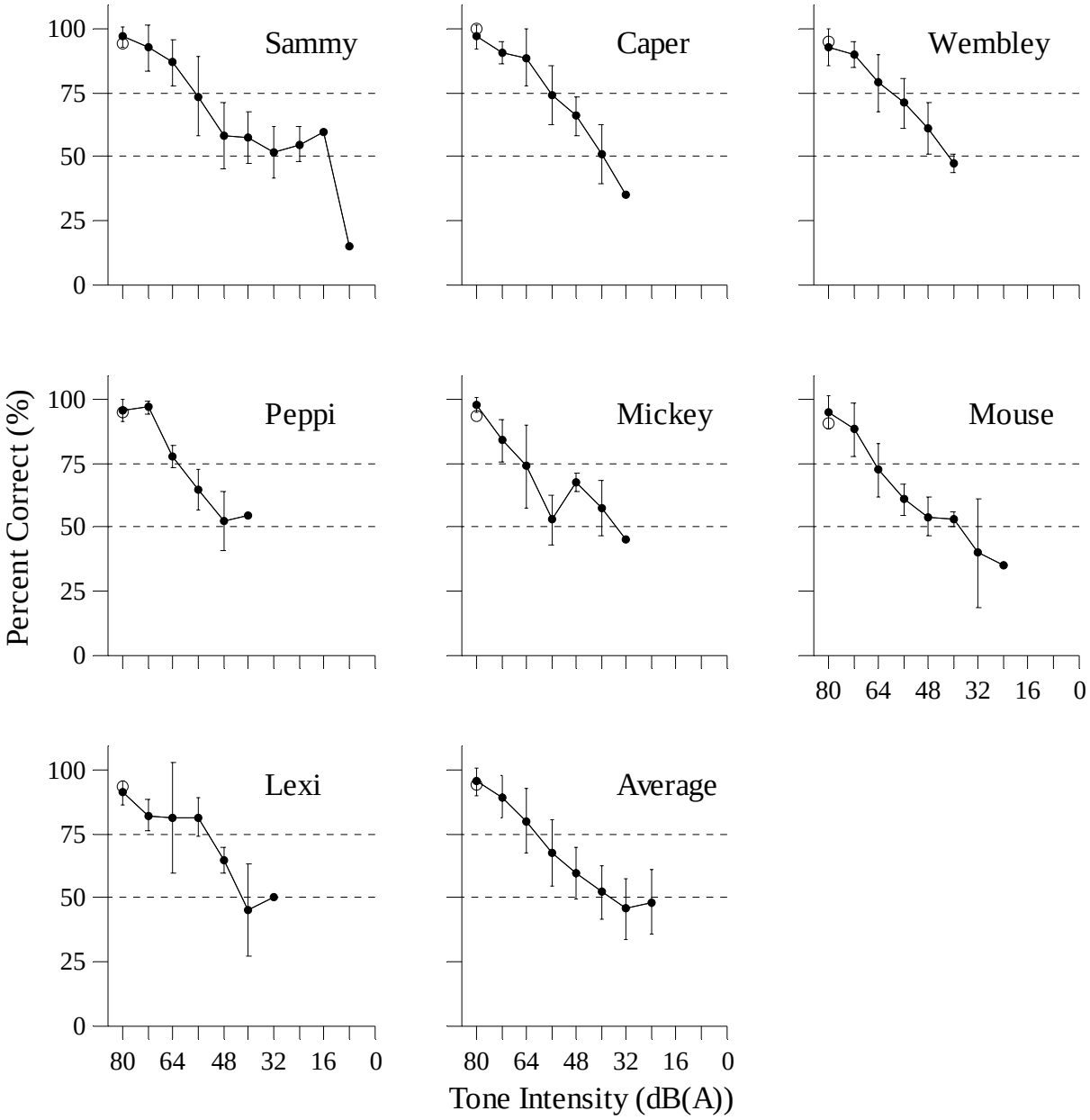

Figure 19. Average percentages correct in overall trials for each possum and for all possums plotted as a function of tone intensity (dB(A)).

for tone-on and tone-off trials, log *d* values, log *c* values and values for ROC analyses.

Figure 19 presents the average percentages correct (filled circles) for each possum and the overall averages across all possums, plotted against tone intensity (dB(A)). The vertical line on each data point indicates one standard deviation from each side of the data point. The unfilled circles are the average percentages correct for the last blocks at 80 dB(A). Figure 20 shows the average percentages correct for tone-on (crosses) and for tone-off trials (filled circles) and the averages across all possums, plotted as a function of tone intensity (dB(A)). In both Figure 19 and 20, the horizontal lines mark 50 and 75% correct. Figure 21 (the left panel) presents log *d* analysis for each possum. Each log *d* value was calculated by using Equation (4) and the Hautus correction, and is plotted against tone intensity. The unfilled circles are log *d* for the final blocks at 80 dB(A). The horizontal lines mark at log *d* of 0.48 and 0. Figure 21 (right panel) gives the ROC plots as is presented in Figure 16. Figure 22 presents average log *c* plotted against the tone intensity (dB(A)) for each possum. The horizontal line marks log *c* of 0. The unfilled circles on each graph show the log *c* value at the final block. Log *c* of 0 indicates no bias towards any levers. Each log *c* was calculated by using the Equation (3) and the Hautus correction.

These figures can be compared with Signal's data (Figures E1, E2, E3 and E4, respectively) which are presented in Appendix E (by the permission of the author) for comparison. The average percentages correct and log *d* (Figures 19 and 21 on the left panel; Figures E1 and E2 on the left of panel) are extremely similar.

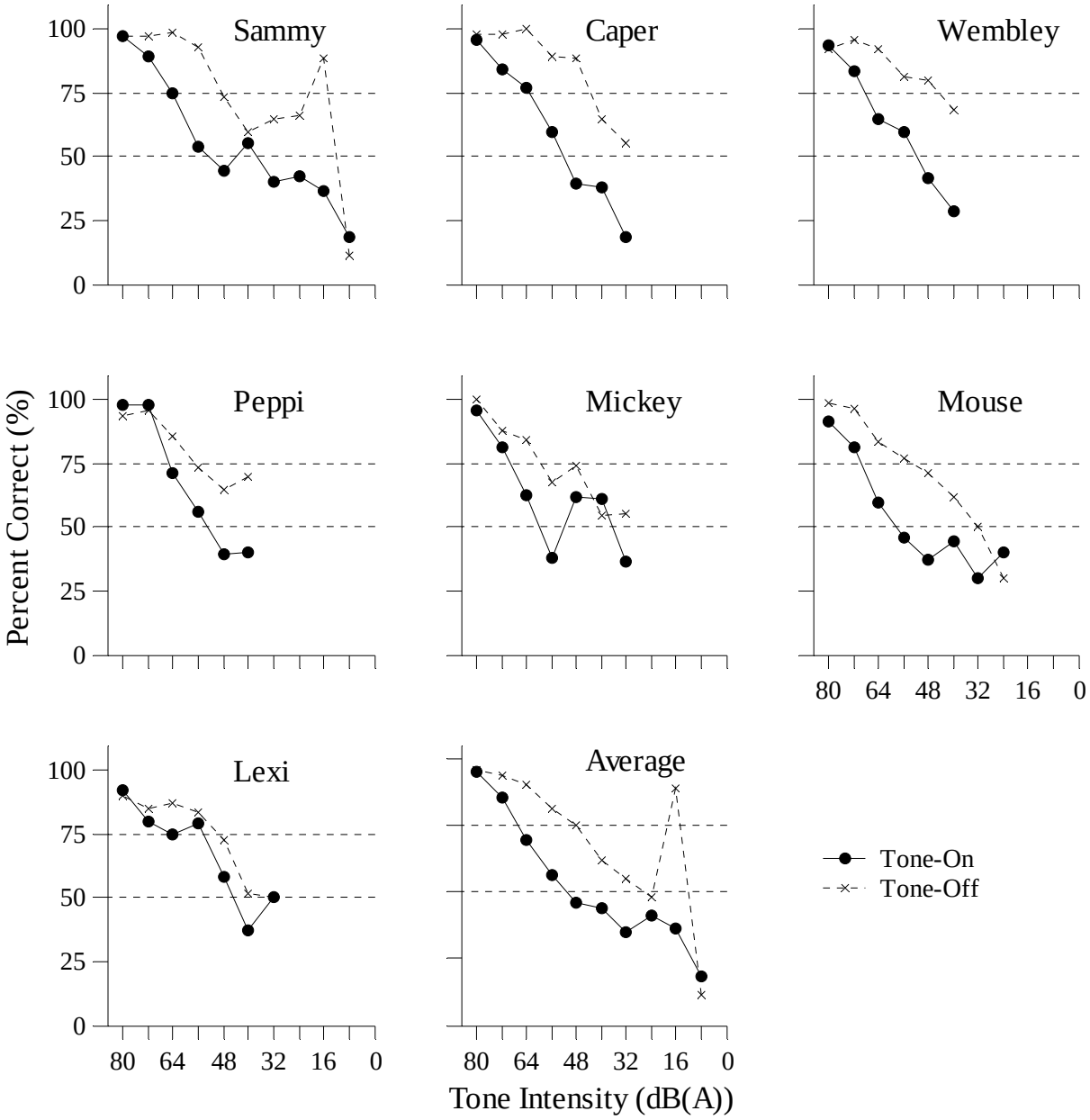

Figure 20. An average performance during tone-on and tone-off trials fore each possum and for all possums, plotted against the tone intensity (dB(A)).

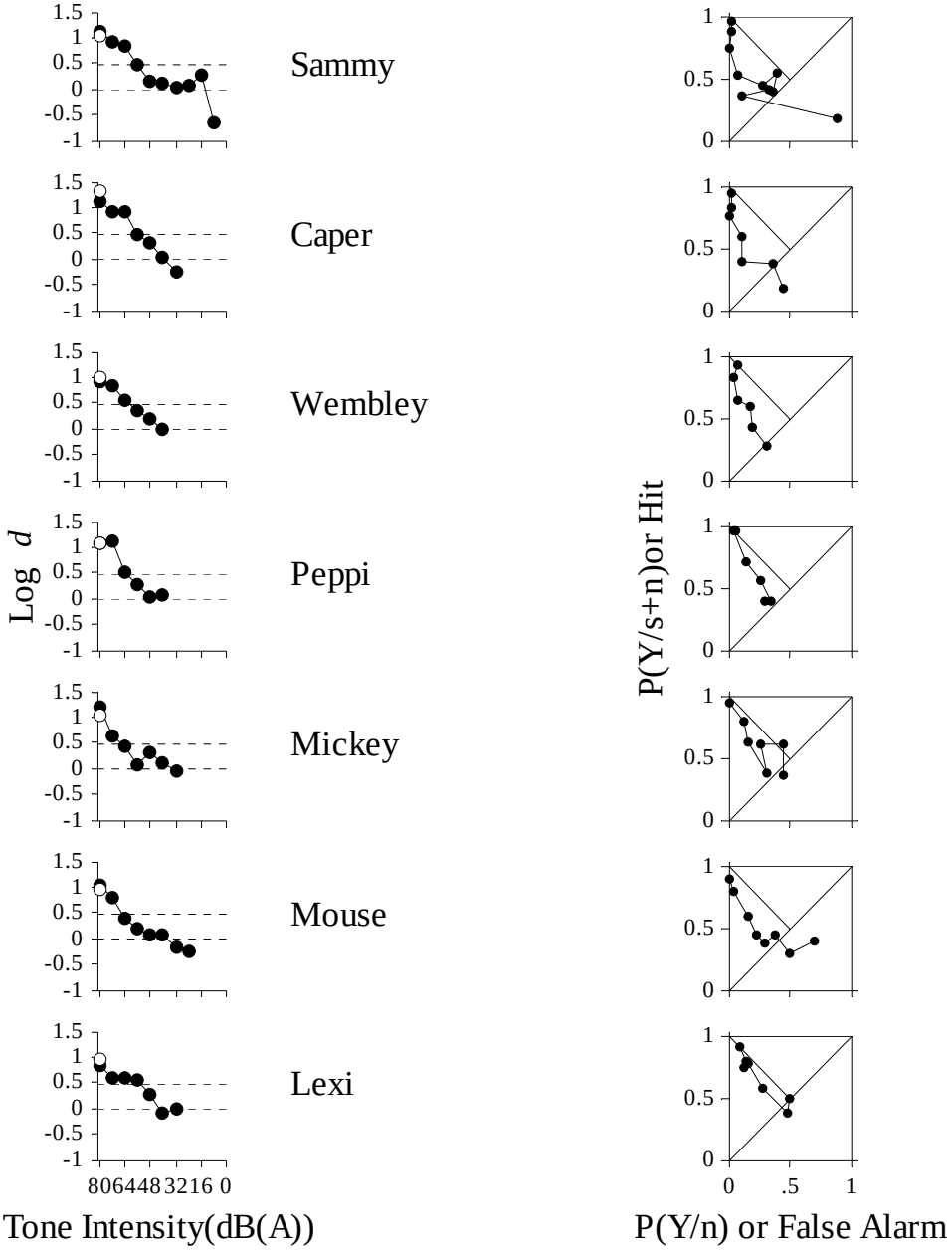

Figure 21. Average log *d* (right panel) and ROC plot analyses (left Panel).

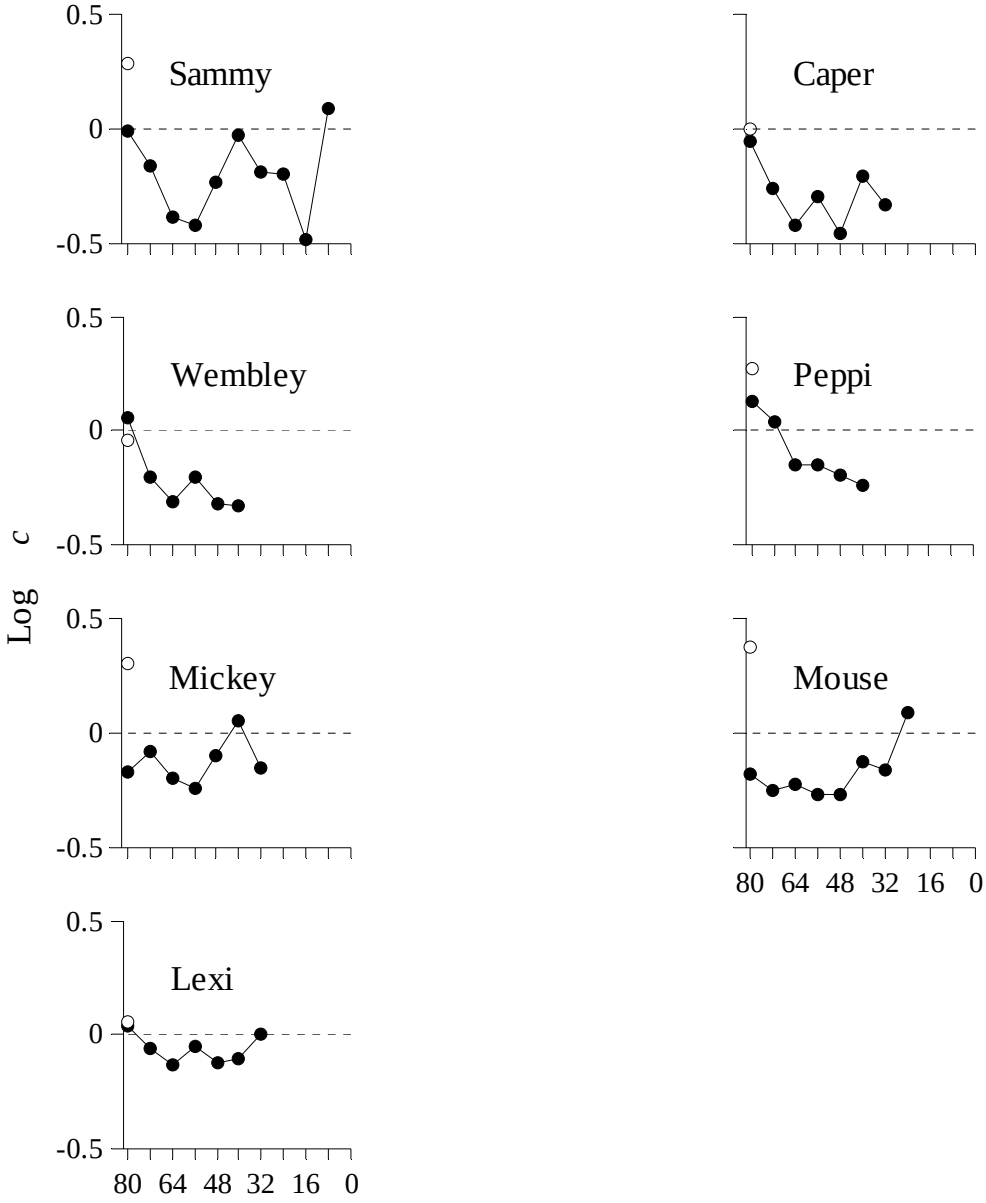

Figure 22. Average log *c* for each possum plotted against tone intensity (dB(A)).

The data from tone-on and tone-off trials (Figures 20 and E4) shows more accurate performance in tone-off trials than tone-on trials in both studies. In both studies, (Figures 22 and E3) log *c* tended to decrease initially and as dB(A) decreased and then increased, reflecting the differences between tone-on and tone-off trials in ROC plots (right panel in both Figures 21 and E2).

Table 4 presents the estimated threshold values (dB(A)) at each threshold criteria, for each possum, and the means (M) and standard deviations (*SD*) at these threshold values across all possums. The second row of each M and *SD* are the results from all six possums in the Signal (2002) study. For comparison with Signal's study each of the five different threshold values were estimated by interpolating from the data points at each side of the criterion value (rather than from a fitted line) of 75% and 50% correct (in Figure 19), 50% correct on tone-on trials (as shown in Figure 20), and 0 and 0.48 in log *d* (as shown in left panel in Figure 21). Therefore the threshold values were found at which the line connected each data point in Figures 19 to 20 as they crossed the horizontal lines at these threshold criterions.

There are occasions when the data line crossed a criterion value twice (i.e., the 50% correct line for Lexi in Figure 19; the 50% correct line for Mickey and Lexi in Figure 20; the log *d* of 0.48 line for Mickey, and the log *d* 0 line for Lexi in Figure 21). In such cases, Signal took the higher dB(A) level, at which the line crossed the criterion value the first time, as the threshold value. In some cases here, no data point fell below the threshold criterions (i.e., Peppi at 50% correct line in Figure 19 and at log *d* of 0 in Figure 21), and the threshold values in such cases were not

Table 4.

The estimated thresholds (dB(A)) at each different criterion from each possum, and of which means and standard deviations for all possums.

	Threshold Estimates				
	75%	50%	50% Tone-On Trials Only	Log *d* of 0.48	Log *d* of 0
Sammy	56.84	14.22	52.78	55.18	13.72
Caper	56.53	39.50	52.06	55.02	39.49
Wembley	60.00	41.46	51.65	59.32	40.99
Peppi	62.15	-	50.00	62.22	-
Mickey	64.8	35.20	59.86	64.9	34.82
Mouse	65.26	38.00	58.49	65.05	38.15
Lexi*	57.85	42.00	44.84	57.54	42.00
M	60.49	35.06	52.81	59.24	34.86
From Signal(2002) [a]	64.09	36.07	54.37	64.81	36.23
SD	3.66	10.51	5.09	4.97	10.66
From Signal(2002) [b]	3.39	9.39	4.44	3.26	9.40

Note. Dashes indicate cases where no values were obtained. Asterisk indicates that the possum's average values are calculated from only four probe sessions. [a] These means and [b] standard deviations are from Signal T.D. (2002). *Assessing Psychophysical Ability In Brushtail Possums* (p.108), The unpublished Doctoral dissertation, the University of Waikato. Adapted with permission of the author.

obtained. Therefore, the means and the standard deviations of the thresholds were calculated by using the available data, only. The estimated threshold values at 75% correct are similar to that at log *d* of 0.48. Similarly, the threshold values at 50% correct for overall trials are also similar to that at log *d* of 0. These findings are also similar to these threshold values found in the Signal's study.

All results from the current study are very similar to those of the Signal (2002) study. Based on her data analyses, Signal concluded that her possums had a bias towards the left lever (correct response for tone-off trials), and the current results support this finding.

One concern in the present study regarding comparison of results with the Signal's study was that the current study obtained a smaller number of probe sessions than Signal did. However, both studies gave similar findings. Thus the current study shows that 4 to 7 probes might be sufficient to estimate threshold values. Another concern was the difference in the cut-off criterion for Wembley and Peppi in the current study. Two threshold values for Peppi could not be calculated in the way Signal did. The cut-off criterion should not have been increased to 60% for Wembley and Peppi, if full comparison with Signal's study had been the goal.

Bias

Across all tone frequencies log *c*, ROC and the percentages correct (for tone-on and tone-off separately) analyses indicated that possums had a bias towards the left ('no') lever. That is, the possums performed generally less accurately during the tone-on trials than tone-off trials. These findings were similar to those reported in other psychophysics studies such as Signal (2002) with possums, DeMello (1989)

from visual discrimination study using hens, and Terman (1970) from the auditory discrimination study using rats.

Terman (1970) reported that animals responded more to the 'no' lever as the task became more 'difficult.' That is, the disparity in percentages correct between two trial types increased as the tone intensity decreased. The data in the current study generally agree with Terman's (1970) findings. However, for some possums, only small levels of disparity occurred at the lowest tone intensity. Moreover, if the 'difficulty' of the task was related to the level of disparity, then the smallest level of bias across all tone intensities at 15 and 20 kHz should have occurred, because the response accuracies were generally high across tone intensity at these frequencies (see Figures 12 and 13). It can also be seen in log *c* and the ROC analyses, the bias and the level of the disparity was very small at the 20 kHz condition across all tone intensities, but in comparison with the 30 and 35 kHz conditions, the bias and the disparity was larger at 15 kHz across all tone intensities than 30 and 35 kHz. It may be possible that the 'difficulty' of the task may relate to the level of the disparity, but it might also be possible that these may have reduced as the tone frequency increased. However, it must be noted that in the current study, apart from the first two probes for Caper, at higher frequencies (over 15 kHz), the tone intensity did not reduce below 24 dB(A). Thus, it might be possible that the possums had not been exposed to the 'difficult' tasks at the lowest tone intensity at the higher frequencies, and the level of bias and disparity remained low.

Signal (2002) considered it was odd that the results that the response accuracy for tone-off trials reduced less steeply than tone-on trials across tone

intensity. In a probe while the tone intensity for tone-on trials reduced across blocks, the tone-off trials always remained the same. Signal (2002) considered that this difference might have occurred because the possums might have perceived the faint tone-on trials as tone-off trials. Signal (2002) conducted another study in which she measured the differences in the possums' response accuracy in 10 tone-off trials, after presenting 10 tone-on trials with faint tones (at 40 or 0 dB(A)). She also measured their response accuracy during 10 tone-on trials with the two faint tones after presenting 10 tone-off trials. In all cases, the session started and ended with a normal block of trials (a 40 mixed tone-on (80 dB(A)) and tone-off trials). She found that presenting tone-on trials first only affected the response accuracy of the possums during the remaining tone-off trials. This did not carryover to the normal block of trials. She concluded that during this block of mixed faint tone-on and tone-off trials, the possums' response accuracy reduced indicating that the possum could not detect the presence of tones well. Thus, the possums may have perceived the faint tone-on trials as tone-off trials. During the tone-off trials and the 'apparently tone-on' trials, the possums responding on the 'no' lever would not always lead to a feedback beep, which only played when a possum made a correct response on a side-lever. Responding on the 'yes' lever occasionally lead to the beep. This indicates that the 'yes' lever response was intermittently reinforced during these trials. Thus, in a probe the possums responding on the right lever increased on tone-off trials as tone-intensity reduced over time. Therefore the response accuracy for both tone-on trials and also tone-off trials reduced as the tone intensity reduced. However as shown in log *c* and ROC analyses, the possums

generally has a bias towards the left lever indicating that the total number of the left lever response would remain larger than the total number of the right lever response.

One problem with the current procedures, in relation to the left-lever bias is that sometimes there was a different number of tone-on and -off trials in each block in probes. In a block, the total number of trials was always 20, but the number of each trial type varied between 8 and 12. If a block contained more tone-off trials than tone-on trials, the overall accuracy of responding in the block would be higher than if there were more tone-on trials, or the equal number of each type of trials. In contrast, if a block contained more tone-on trials, then the overall accuracy of responding will be lower than if there were more tone-off trials, or the equal number of each type of trials. However, the number of trials of each type varied across blocks, and this study used the average across all probes for each measures. Therefore, it should have not given rise to a consistent effect on the overall data at any frequencies. Also the use of the best fitted regression line as a means of describing the trend should reduce any effects of having a different number of trials of each type, and it should provide a good estimate of the performance.

Procedural Concerns

Replicated Conditions

Iinitially, the tone frequency was increased over conditions from 880 Hz to 10 kHz. At this point, both the 880 Hz and 2 kHz conditions were replicated to investigate if there were any order effects or learning effects across conditions. In both cases there was a slight improvement in response accuracy for all possums

across all tone intensities at the second exposure. This suggested that there had been some learning effects and that the possums had learnt to respond more accurately in probes across conditions. However, the overall response accuracy in the 2 kHz condition was still higher than in the 880 Hz condition. This suggests that the possums overall response accuracies were mainly affected by tone frequencies.

Sound Equipment

Change in the 15 kHz Condition. To ensure the type of speakers used in the 15 kHz condition for different possums did not affect the performance of the possums, two possums were exposed to the 15 kHz condition twice, firstly with the modified speaker and secondly with the tweeter. The results showed a slight improvement in the overall response accuracies across blocks during the repeated condition compared with the initial condition, which was similar to that observed during the repeated 880 Hz and 2 kHz conditions. Thus, this might have occurred either due to the learning effects or due to the use of the different types of the speakers. However, the results indicated that the effect was small and so the use of either the tweeter or the modified speakers did not affect threshold values greatly.

Testing Calibrating procedure in the 20 kHz Condition. To ensure that the use of the calibrating procedure would not affect on the possums overall performance, the 20 kHz condition was repeated for some possums. The results showed, except for Mickey, the shapes of the functions were similar between these two conditions. This indicates that at 20 kHz the use of either the standard or the calibrating procedure did not change the response accuracy greatly. However, as can be seen in Figures 17 and 18 across all possums, the threshold values from the

first exposure were lower compare with the threshold values from the second exposure. As mentioned in Appendix B, the tweeter produced static noise during the initial 20 kHz condition. The noise was constant in both tone-on and -off trials, and thus it could have predicted to reduce response accuracies for the possums. However the response accuracy was greater when the tweeter produced noise. The static noise increased in volume when the power (the volume dial) to the tweeter was turned up. Thus this might indicate that the tone intensity in the initial 20 kHz condition was higher than it was in the second exposure, as the tweeter did not produce noise during the second 20 kHz condition. Also as it was also mentioned in Appendix B, 20 kHz is outside of the dB(A) meter's optimal frequency range. The dB(A) meter measures tone intensities lower outside of this range, thus this would be another reason that the sound set with the dB(A) meter in the initial 20 kHz condition might be higher. Figure 11 also suggests that the intensity might have been higher than it was measured in the first 20 kHz exposure, because most possums' percent correct did not decreased below 75% accuracy, and probe sessions terminated at the nominal 24 dB(A). Thus, it might be possible that due to the tone intensity might have been higher in the first exposure, the overall threshold values were higher.

Data Analysis

In the current study, the average data for each measure was used and presented as there was no consistent difference across all probes for each possum at each tone frequency. As mentioned earlier, any blocks of trials for which there were only one or two data points, were excluded. That exclusion was to prevent the

misinterpretation of the overall performance of the possums. For instance, if there were only one or two data points with high response accuracies at a low intensity value, then including such data in a possum's average performance would have biased it to suggest that the possum always performed well at this low tone intensity. This also may have overestimated the hearing ability of a possum when calculating the threshold values. The other type of data being excluded was for blocks in which if tones for tone-on trials was reduced and presented at 0 dB(A). This was because in this block the stimulus presented in both trials types was assumed to be the same hence this should not be considered a discrimination task.

Audiogram

To estimate threshold values, the criterion of 75 % correct in the overall percentages correct analysis and a log *d* of 0.48 were used. These threshold values were calculated based on the linear regression lines that were fitted on each graph. In both percent correct and log *d* analyses, with a visual inspection the linear regression line fitted better for each set of data compare with a curvilinear regression line. Another common way to estimate the threshold values would be to use the threshold criteria of 50% correct from the percentages correct analysis for tone-on trials only. This audiogram was not presented in this study would have had a similar shape to that in Figure 17, but with lower threshold values. In fact there were many negative threshold values especially at the higher frequencies. This is because the most of the data points in Figure 13 were over the 50% correct line, and thus the best fitted linear regression line did not cross the 50% correct line at positive tone

intensities. This resulted in negative threshold values, which were clearly meaningless and were, therefore not presented.

Concern with the 15 and 20 kHz Conditions

The threshold values in the 15 and 20 kHz conditions were very low for all possums (see Figures 17 and 18). Initially it was considered that this might be the result of a technical problem, in that the sound pressure had not been reduced accurately across blocks. To assess this, the tone intensity was measured across blocks using the dB(A) meter, and it was found that the tone intensity was reducing appropriately. It appears from the data that the hearing sensitivity could have been high at around 15 and 20 kHz. However, as mentioned before, this must be viewed with caution in that the tone intensity in these conditions was higher than measured by the meter.

Technical Concerns

As the current study involved the production and measurement of tones that were above the normal human hearing range, there were some technical difficulties. One concern with this study was the accuracy with which the tone intensity could be set and measured. According to the instruction manual of the dB(A) meter, the most optimal frequency range for the meter was determined by measuring tone intensities at different frequency ranges at 1 m away from the sound source (i.e., a speaker) while the microphone was directly facing at the speaker. In the current study, the dB(A) meter was placed at a location that would be approximately the same distance to the location where the possum's ear would be positioned during the experiment. The distance from the speaker to the location where the microphone was placed was

shorter than 1 m. Due to the location of the microphone as it was set to measure tone intensities, the dB(A) meter was not facing the speaker. Thus a possum ear might have received a different tone intensity to that measured by the dB(A) meter, because the meter was not placed appropriately when the tone intensity was set. In addition, there were problems in measuring tone intensity when the frequency was outside of the optimal range for the sound pressure meter (31.5 to 8 kHz). The further the frequency is from this range, less accurately the meter reads. Therefore especially at the high frequencies, the tone intensity set for each session may have not been accurate (see more detail in Appendix B).

The second concern was the use of the calibrating procedure and the dB(A) weighting scale. As mentioned in Appendix B, the dB(A) scale was used in this study because it is of an international standard. Furthermore, a sound pressure meter using the dB(A) weighting scale can easily be obtained anywhere. However, it becomes problem when measuring tone intensity at over 20 kHz. The dB(A) weighting scale is based on human hearing, and the dB(A) meter itself functions only up to 20 kHz. The use of the calibrating procedure was an option for setting the tone intensity over 20 kHz (see Appendix B for more detail). Using the calibrating procedure, tone intensity was assumed to be at 80 dB(A) but the accuracy of this assumption could not be assessed for these high frequencies tones (30 and 35 kHz), because equipment was not available to do so during this study. The best way of setting tone intensity at these high frequencies would be by using an appropriate weighting scale (i.e., dB(SPL)). This should be the approach for any future study.

The third concern was the accuracy of high frequency tones. Sound waves of high frequencies can be distorted by the surrounding environment such as changes in humidity, the presence of other sounds, or the sound waves themselves. For example, in humid air conditions, more sound pressure is required to play tones with the same volume than in dry air conditions. Also the sound waves could be distorted by the noise made by the presence of other possums in the experimental room. The noise level in the laboratory was between 28 and 50 dB(A) depending on what noise possums were producing. The sound waves, especially at higher frequencies, can be reflected on any object (e.g., wall), and typically the reflected sound waves can influence the sound waves just produced from the speaker. For all these reasons, the tone stimuli presented for the possums may not been constant through out a session.

The fourth concern was the position of possums during the experiment in relation to the problem with higher frequency tones. Sound, especially at high frequencies, is directional and thus the tone intensity measured at different places in the experimental chamber (also their housing cage) was often different. In this study, the possum's head was not restrained, thus the tone intensities that possums received would depend on where their ears were positioned and which direction they faced. Signal (2002) studied and compared a possum's performance with the 880 Hz tone in two different testing environments, either in a sound attenuated chamber, or their housing cage (same environment as the current study). She found no difference in the data collected in these two testing environments. However, the 880 Hz tone was a low frequency and it may be possible that the sound waves would have been distorted by the surrounding environment only minimally. Thus, in the future the

use of a sound attenuating chambers are recommended, with walls that prevent reflection of sound waves, and hold a constant humidity especially when testing higher frequency tones.

The last concern occurred in the 100 Hz condition, where the vibration of the speaker while tone was played might have been problematic. As the speaker was attached to the cage, the vibration transmitted to the cage while the tone was playing. Such vibration may have helped the possums detect the presence of the tone. However, high threshold values were found at 100 Hz, suggested that these effects if any were small. Repeating this condition by placing the speaker independently of the cages to prevent the transmission of the vibrations to the cage is recommended for future study. In addition, while the tone was played, the air vibrated which was sensed by the experimenter. The air vibration is unavoidable for tones at low frequency. If this could be detected by the possums, it would be an empirical question which would be whether the possum have detected the air vibration or the tone would be arisen. However, if the possums could detect the vibrations in the air better than the presence of tone (by perceiving tones by their auditory systems), then it would predicted that the response accuracy would have increased. As presented, the threshold values at 100 Hz were the highest in this experiment, thus this was not the case in this study.

Conclusion

In conclusion, despite the many technical issues involved in this study, the current study measured and presented the hearing ability of possums. The possums could hear tones ranging from 100 to 35 kHz, with most sensitivity shown to tones

between 15 and 20 kHz. Until now, there was very little known about hearing abilities in possums or their psychophysical ability. This study, in spite of its limitations, contributed to the psychophysics information on the possums. As it was mentioned by Brockie, et al. (1984), to control the possum population effectively using currently applied methods, more research is required. Research on sensory ability of possums was one of such required area of research by Clout and Sarre (1997) and Wynne and McLean (1999). More particularly very little research has been completed on possums hearing ability (Signal, 2002). Thus, this study has added knowledge about the auditory ability of possums and it may contribute to the control of the possum population more effectively. Carey, et al. (1997) suggested adding an auditory lure to a standard bait station to attract possums to the bait station. As the current study investigated the hearing ability of possums, it is thus possible to determine which sounds might be added to the auditory lure, in the future.

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APPENDIX A

The determination of which speaker to be used for different frequencies

For the purpose of this experiment, two different types of speakers were used to play tones at different frequencies. One type, Digitor indoor/outdoor speakers (A9774) measuring 121 mm x 191 mm x 197 mm, could produce tones between 70 and 20000 Hz. Each speaker consisted of three different internal speakers (a woofer, a midrange and a tweeter) connected with a crossover driving the midrange speaker and the tweeter together. A capacitor was used as a high pass filter, and so no low frequencies passed to the tweeter and the midrange speaker.

The other type were Foster ribbon tweeters (CT2023) with the optimum frequency range of approximately 3.3 to 50 kHz at 80 dB(A). When in use, each tweeter was attached to a plastic panel that replaced the three internal speakers of the Digitor speaker.

To make sure each type of speakers and the sound equipment used for the present study produced the tones accurately, each tone frequencies used in the experiment, between 100 and 35000 Hz, was measured and analyzed using two sound measuring procedures.

One procedure was to observe the sound waves generated from each speaker. The sound waves were received by a microphone (Sennheiser 21/22) situated approximately at the distance the possum's ear would be from the speaker. The sound waves were converted to an electric current and sent to an oscilloscope (Kikusui 40M Hz COS 5040^{TM}) that was attached to the microphone. The optimal frequency for this microphone was up to 20 kHz, although the performance deteriorated at high frequency and it did not receive sound waves over 12 kHz accurately. To observe the sound waves for the tone frequency higher than 12 kHz, the Foster ribbon tweeter was used as a microphone. By operating the tweeter in a reverse direction, connecting the electric wires to the oscilloscope's inputs, the tweeter could receive the sound waves and generate an electric current to be measured by the oscilloscope. The sound waves from high frequency sounds could be easily disrupted by the surrounding environment (such as humidity, wind or other sound), and the receiver (the tweeter) was not sensitive enough to capture sound frequencies from any distance, to ensure tone purity and amplitude, the sound transmitting speaker and the receiver were attached together face to face. Similarly, to measure tone frequency lower than 880 Hz, the Digitor speaker was also used as a microphone as the microphone was unavailable at the time of testing.

The second procedure was to observe the alternating current (AC) signal voltage that was sent to the speakers from the amplifier. A multi-meter (Fluke 79 series, manufactured by John Fluke) was connected in parallel to the speaker to ensure that the same amplitude was measured with each tone frequency. The multi-meter indicated that a signal voltage was sent to each speaker with +/- 1 Hz resolution, and thus each sound frequency was accurately played.

According to both measuring procedures, each speaker was accurate in playing tones in different tone frequency ranges. The Digitor indoor/outdoor speakers could produce tones from 100 Hz to 10 kHz accurately. A modification to these speakers was required to minimize the noise produced from the internal woofer at 12.5. For the modification, only the internal tweeter and midrange speakers were connected. The modified speaker could produced tones at 15 kHz, only up to at 72 dB(A), the detail will be discussed in Appendix B. The Foster ribbon tweeters were shown to produce tones at 15 kHz and up to 35 kHz.

APPENDIX B

Tone intensity was adjusted to 80 dB(A) by using a dB(A) meter (Testo 816) at the beginning of an experimental day or any probe session. According to the instruction manual, the optimal frequency range of this dB(A) meter was 31.5 to 8 kHz, and its performance was said to be deteriorate outside of this frequency range. The use of the dB(A) weighting scale (indicated as 'A' in Figure B1) was considered to be appropriate as it is a widely used scale and equipment to measure tone intensities based on the dB(A) weighting scale (this is based on normal humans' hearing ability) is also widely used and obtainable with a reasonable cost.

Using this procedure and a modified speaker, it was unable to set a tone intensity at 80 dB(A) accurately at 15 kHz. The speaker started to make a static noise and the tone frequency measured was not accurate, and the tone intensity fluctuated a lot. Similarly with a tweeter at 20 kHz, when this tone was played at around 80 dB(A), the intensity measured by the sound pressure meter fluctuate a lot. At the same time, it was found that the tweeter started to make a constant static noise at this volume. In fact this volume destroyed one tweeter. One possible reason for the fluctuations in the meter readings was the simply because the dB(A) meter at there frequency might not have functioned well. Another

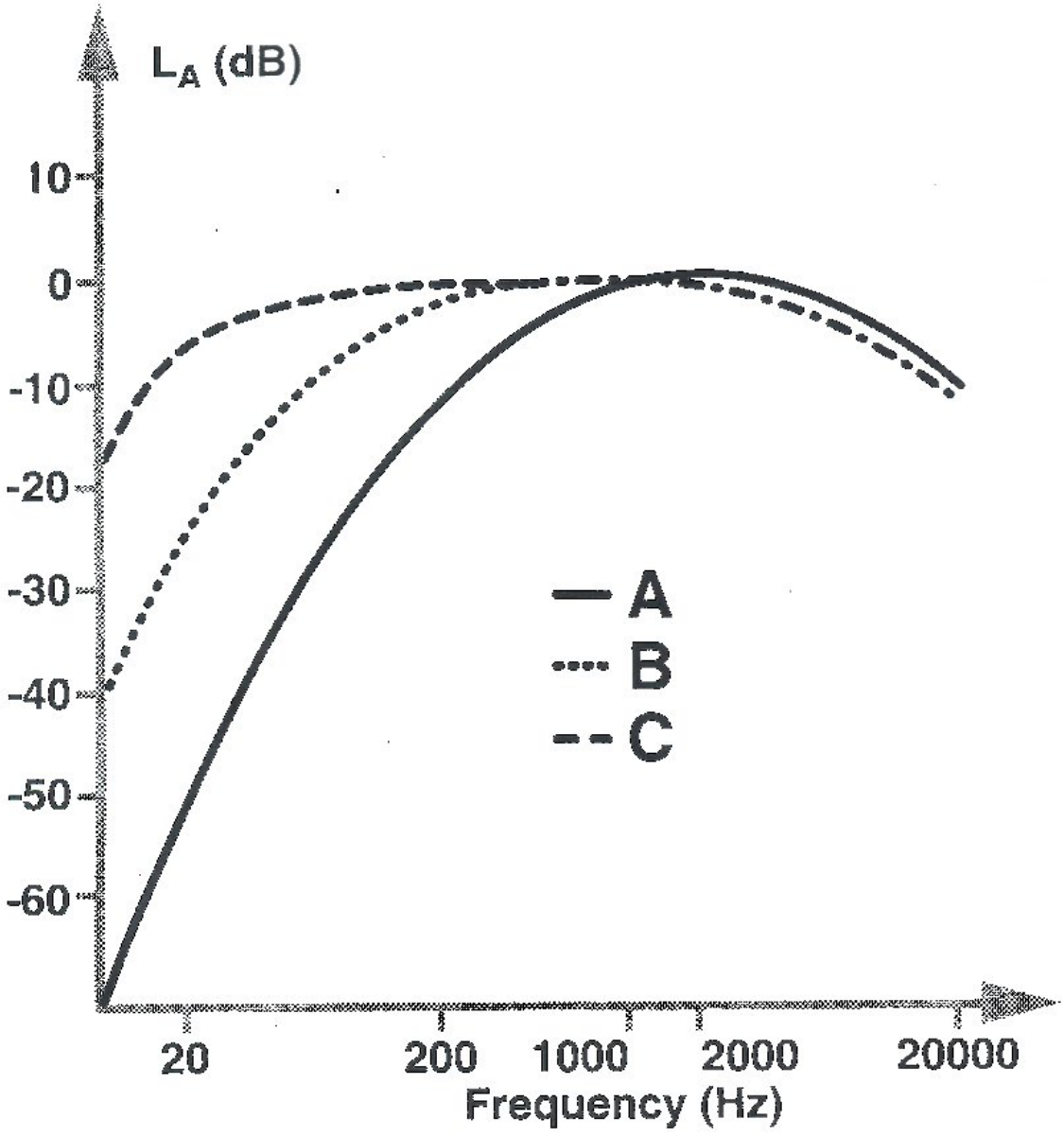


Figure B1. The performance of sound pressure meter, Testo 816, based on dB(A) weighting scale, copied from the instruction manual in June 2007.

possible reason for the fluctuations was the characteristics of sound waves with the high frequency tones. Such sound waves are commonly known as a directional and also easily disrupted by the surrounding environment (i.e., humidity, wind and other sound) and thus this may be the reason for this fluctuation in tone intensity. The reason why there was some static noise and the tweeter was destroyed was because the tone pressure requirement to produce at this frequency at this intensity. That is, to produce high frequency tones at a high volume (i.e., 80 dB(A)) at a certain distance, the tweeter needed to move fast as to produce this frequency and with a strong force to meet the required tone intensity. To do so, the tweeter required a high level of energy input, and due to this the tweeter made a constant static noise, and was destroyed.

At this point, the maximum tone intensity at 15 and 20 kHz was reduced to 72 dB(A), the tweeter was still making a small static noise but both speaker produced accurate tone frequency (as mentioned in Appendix A). Therefore in the experimental condition at 15 and 20 kHz, the maximum tone intensity used for these experimental conditions were 72 dB(A).

There was the other problem with this procedure to set the tone intensity that was the dB(A) meter was unable to measure the tone intensity over 20 kHz.

This was because this range is beyond humans' hearing ability, so most meter are not designed to measure high frequency over 20 kHz.

Ideally a second meter (i.e., Gen Rad 1933 Precision Sound Level Meter and Analyzer) that can measure sound intensity between 5 Hz to 100 kHz but the project did not have the budget to cover the cost of this, nor could not be hired or borrowed. Thus to set the sound intensity correctly, three procedures were considered.

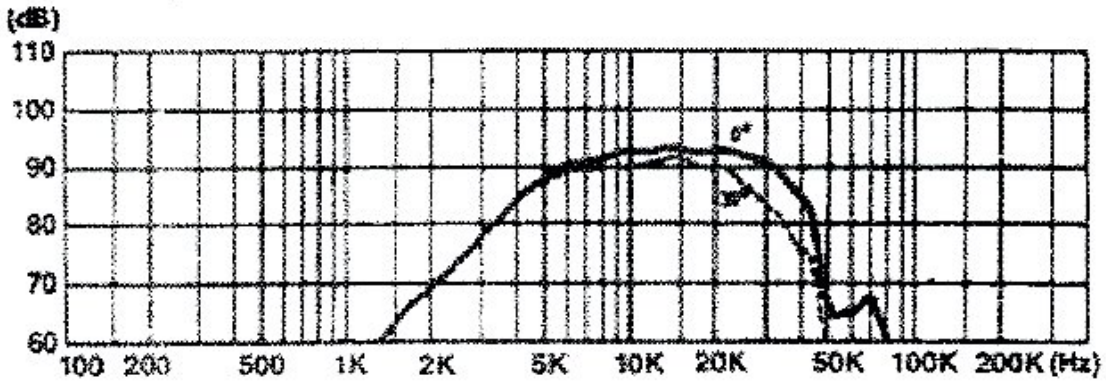
First involved using the Testo dB(A) meter but accepting that there would be some deteriorations in its performance at these frequencies. However, as it was mentioned before, it failed to set the tone intensity accurately even at 20 kHz at 80 dB(A), therefore to measure and to set tone intensity at the frequency over 20 kHz using this meter was not possible.

The next idea was to build a new sound pressure meter with the tweeter as a microphone. The device had a meter to indicate the sound pressure. Although theoretically this should have worked but the one produced failed to measure the sound intensity over 20 kHz accurately.

The third option was to calibrate tone intensity at 7 kHz, at the middle of 6 to 8 kHz, which is the most functional frequency of both the tweeter and the sound

pressure meter. As it can see in Figure B2, the performance of the tweeter was at a constant level between approximately 3.3 to 50 kHz at 80 dB. Theoretically, once the sound pressure was set at a certain level within this frequency range, the sound pressure at any frequency within the same range should remain the same. However, as mentioned before the dB(A) weighting scale does not indicate the relationship between the decibel level (sent from the amplifier) and the dB(A; the sound pressure level produced from a speaker base on human hearing) over 20 kHz. Thus it was an assumption that if the volume was set at 80 dB(A) at 7 kHz, that the speaker would produce sound with the similar sound pressure level at 30 and 35 kHz.

In addition to this procedure, a multi-meter (Fluke 79 Series, manufactured by John Fluke) was used to measure the power input (V) to the speaker when the volume was set to make sure it would not exceed 1.3 V to reduce the risk of the tweeter breaking down.



Nominal Impedance.....8Ω±15%
Nominal Power 20W
Maximum Power 50W
Rated Freq. Range .....6,000~40,000Hz
Sound Pressure Level .....92±2dB/W
Net Weight.....242g(8.54oz.)
Cross Over.....6,400Hz(12dB/oct.)

Figure B2. The performance of the Foster Ribbon Tweeter copied from the instruction manual on November 2007.

APPENDIX C

During experimental conditions, some possums were unable to complete all the training or probe sessions and so there were some alterations in the experimental procedures the 12.5, 30 and 35 kHz conditions.

12.5 kHz condition

During the experimental condition at 12.5 kHz, after Mouse completed two probe sessions, no successful probe session occurred next nine consecutive probe sessions. Inspection of the data showed that in spite of not completing probes Mouse continued to gain as many reinforcers in training as in the probe session. Thus it was possible that reducing the number of reinforces that Mouse could earn during a session may help him complete the probe.

Also the duration for which Mouse made no responses on any levers during each successful and unsuccessful probe session was measured. Mouse paused for more than 3 min in 8 of the 10 unsuccessful probe sessions, and for up to 34 min in a single pause. In 3 of the 10 unsuccessful probes, after having a 16, 21 or 23 min pause, Mouse began responding again. However, these sessions terminated while he was still responding because this reached the 1-hr session time. Thus if Mouse was given a longer session, then it could be possible for him to complete a probe session.

Thus three changes to the procedure in a probe session were made only for Mouse and only in this experimental condition. One change was that the starting tone intensity of a probe was changed to 64 dB(A) from 80 dB(A) to reduce the maximum number of reinforcers that Mouse could earn. This was considered

possible, as Mouse responded with a high accuracy of between 75 to 100% correct in blocks at 64 to 80 dB(A) during both the successful and unsuccessful probe sessions at this frequency. The second change was to reduce the amount of the supplemental feed by 40 g (20 g of dock leaves and 20 g of apple) on the day before a probe day. However, to keep his weight constant, an extra 40 g of supplemental feed was given on the probe day with his daily supplemental feed.

The third change was to extend the length of a probe session until either Mouse completed a probe session, or until he had not made any responses for more than 30 min.

After these changes were made, Mouse completed remaining three probe sessions successfully.

30 kHz Condition

During the training in the 30 kHz condition, Mickey and Mouse did not reach the training criterion after completing 39 and 30 sessions, consecutively. Both possums had responded at 85% correct or more for over five consecutive sessions, above a chance level, indicating that these possums were discriminating between tone and no-tone stimuli. At this point, probe sessions were conducted for these two possums when they responded over 85% of the trials correctly in a preceding training session. The criteria for a successful probe session remained the same.

35 kHz Condition

As Mickey and Mouse did not reach the standard training criterion in the 30 kHz condition, thus their training criterion in 35 kHz condition was changed to 85% or more correct for five consecutive sessions. The required response

accuracy for a preceding training session before a probe was also changed to over 85% correct.

APPENDIX E

Figure 7.4, 7.5, 7.6 and 7.7 copied from Signal (2002) with the permission of the author, in this study each figure was labeled as Figure E1, E2, E3 and E4, respectively.

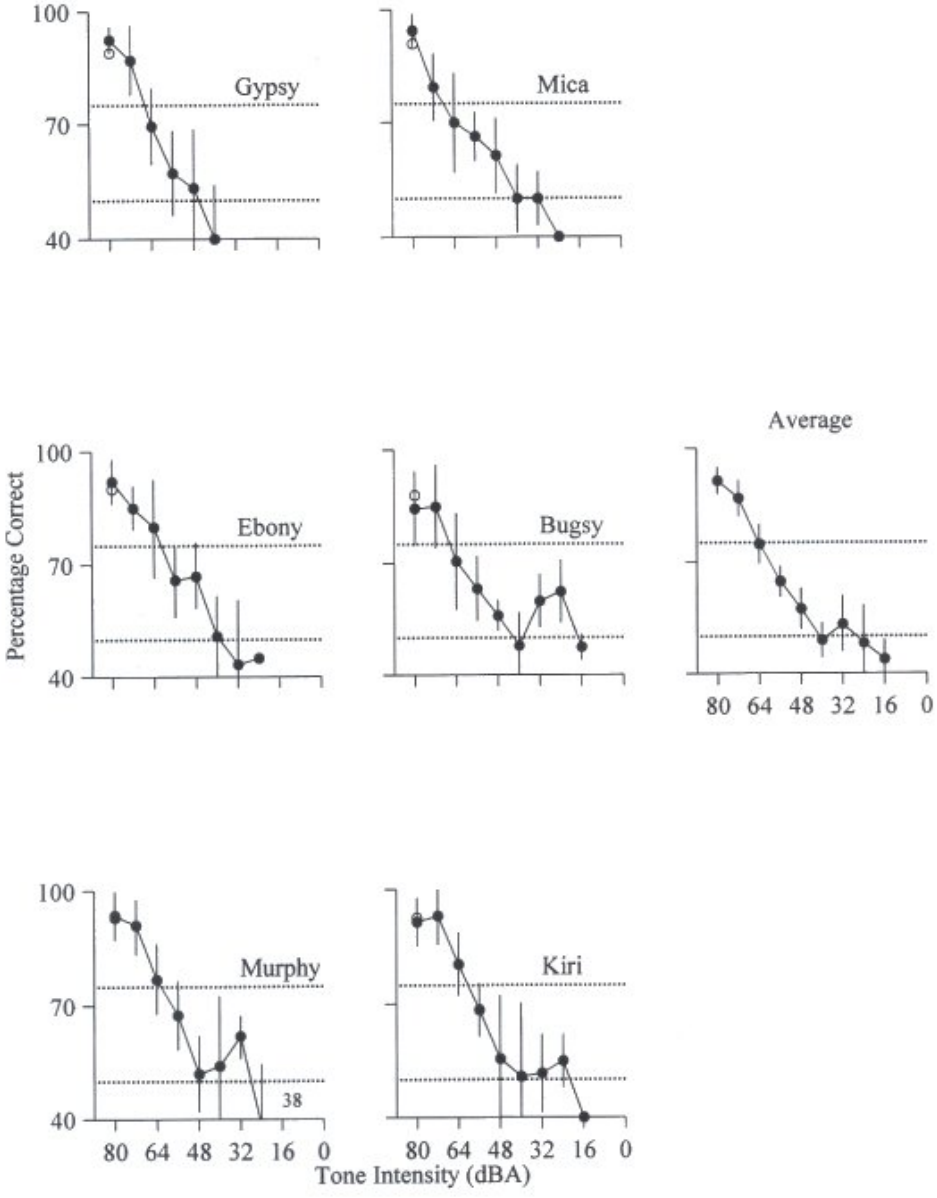


Figure 7.4. Average percentage correct gained over 10 threshold sessions as a function of tone intensity (dBA).

Figure E1. Average percent correct measure from Signal (2002).

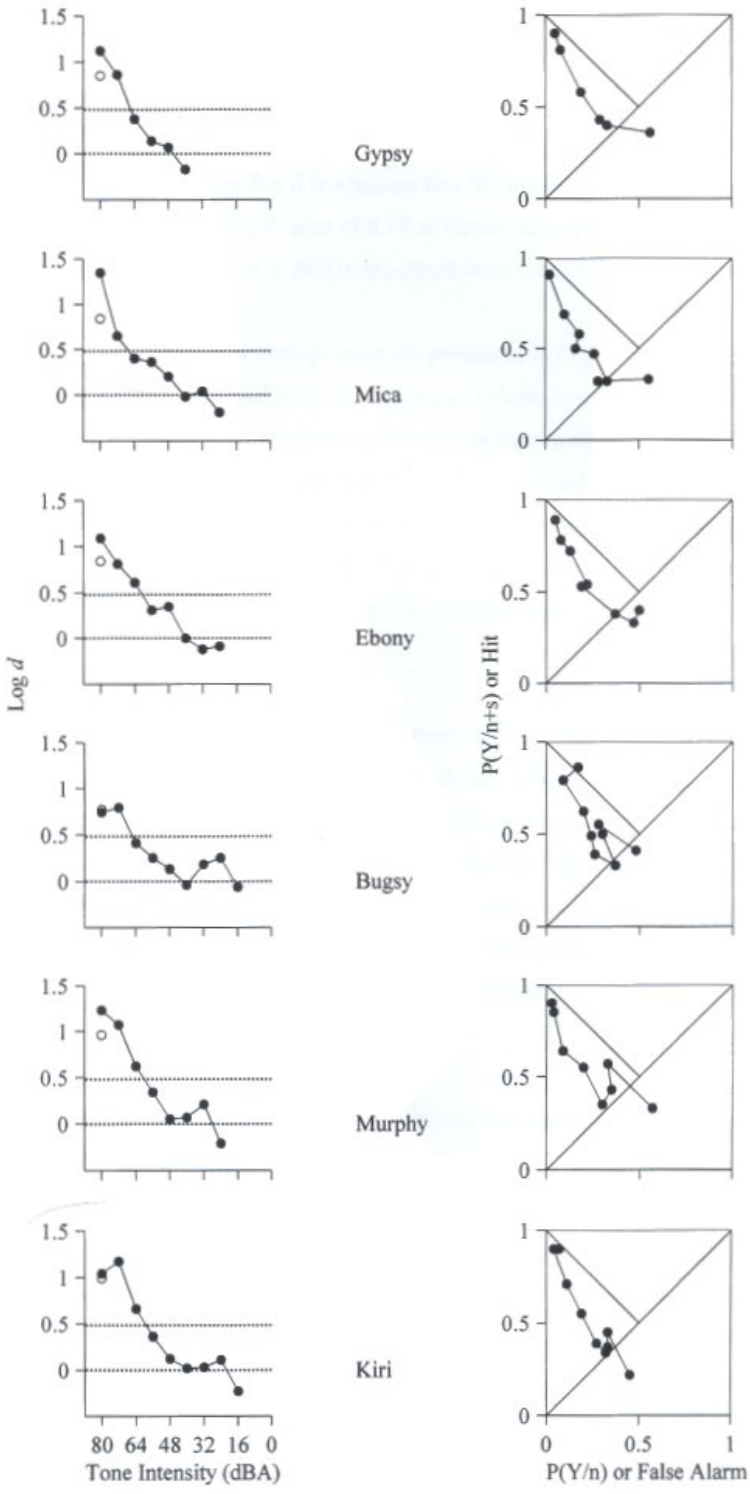


Figure 7.5. Log *d* and ROC plots of data averaged over 10 threshold sessions.

Figure E2. Log *d* and ROC plots from Signal (2002).

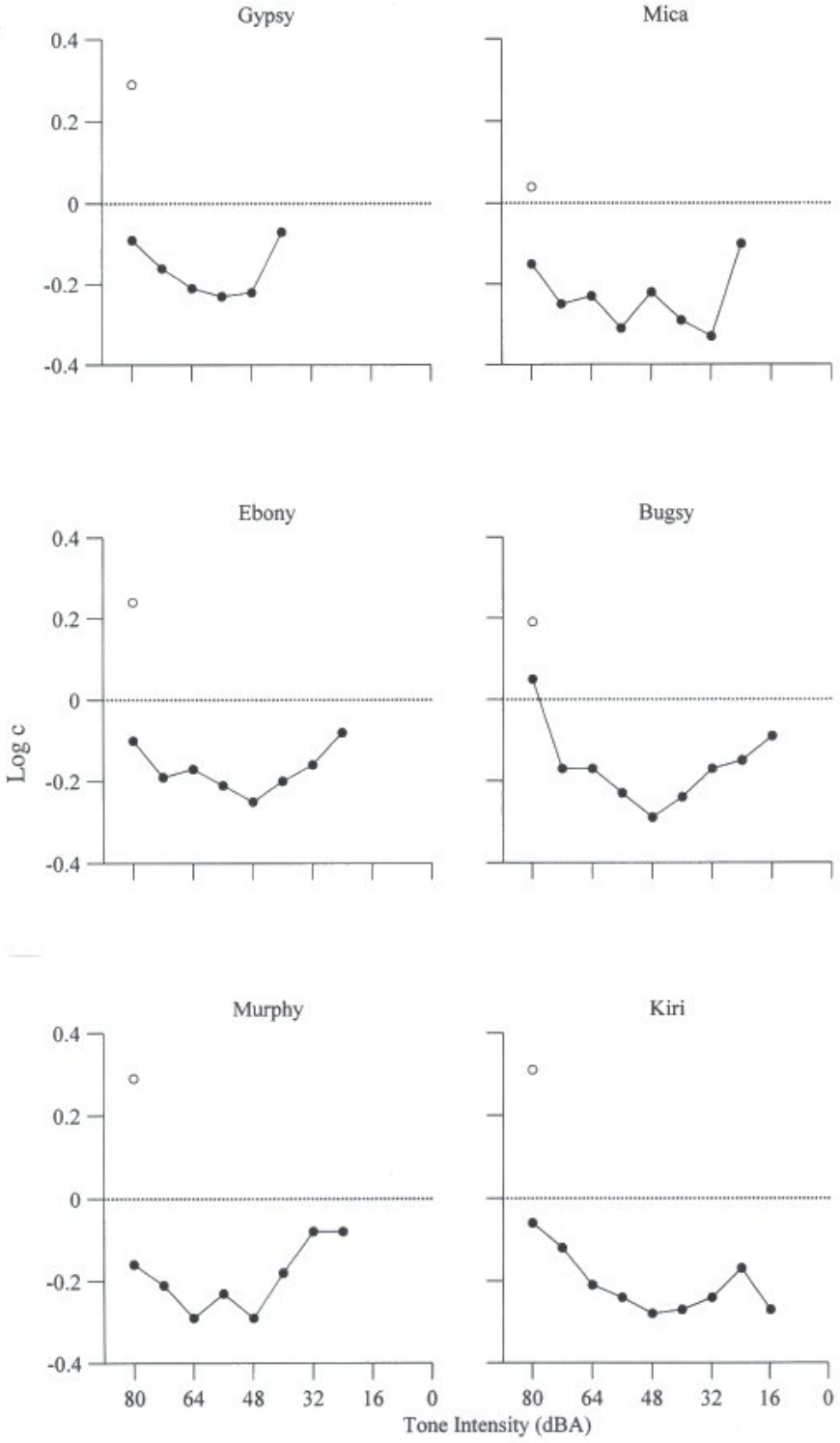


Figure 7.6. Log *c* analyses (with Hautus correction) of average data from 10 threshold sessions.

Figure E3. Log *c* from Signal (2002).

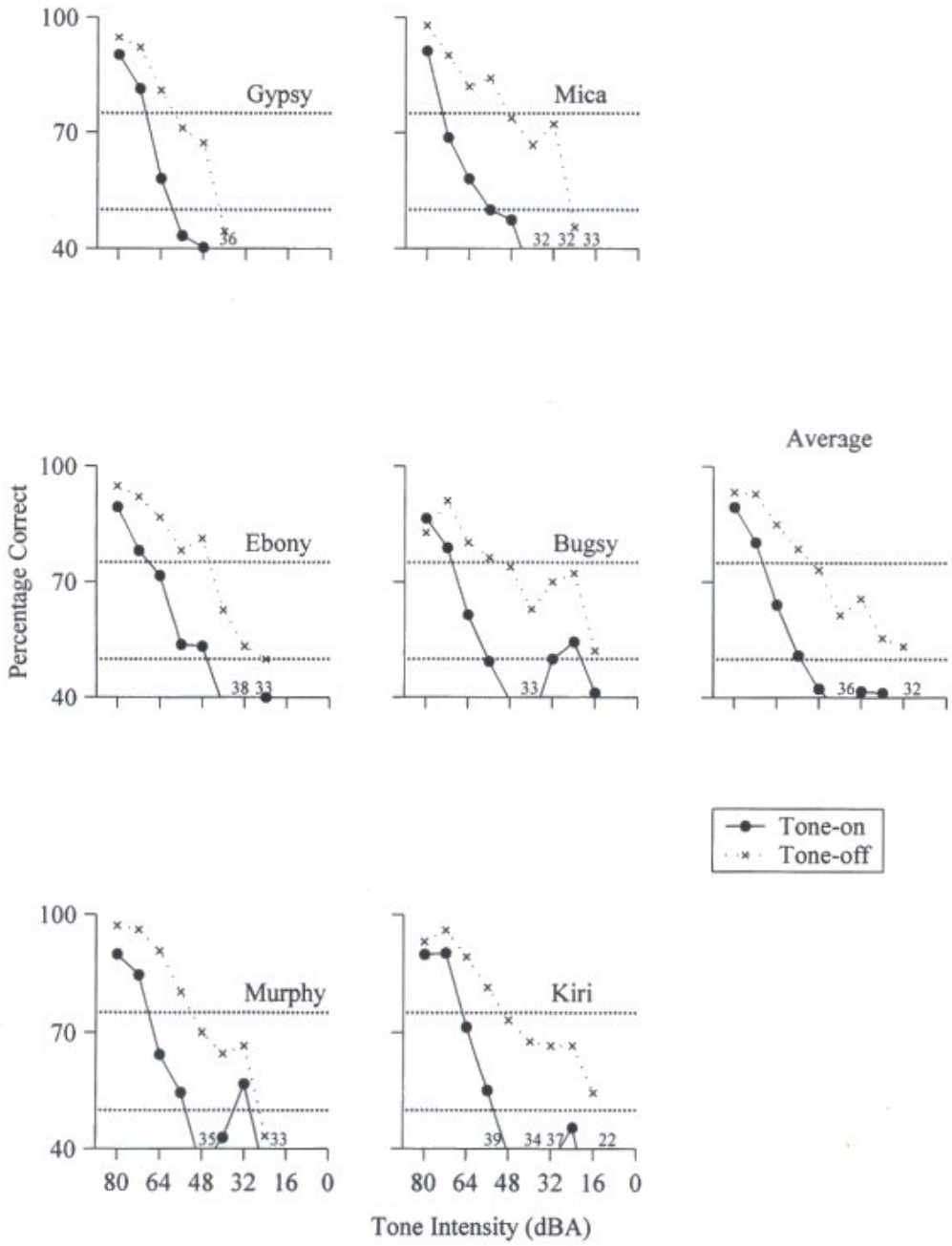


Figure 7.8. Percent correct gained on tone-on and tone-off trials separately presented as individual averages and averaged across possums as a function of tone intensity.

Figure E4. Average percent correct measure on tone-on and –off trials from Signal (2002).